Part

B

Section 5: Ecological Risk Analysis for the Marbled Murrelet: The Sensitivity of Viability to the Parameters of the Zone-4 Metapopulation Model

Ecological Risk Analysis for the Marbled Murrelet: The Sensitivity of Viability to the Parameters of the Zone-4 Metapopulation Model

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Executive summary

1. I analyzed of the metapopulation dynamics of the Marbled Murrelet in conservation zone 4 with a stage-structured, stochastic metapopulation model of the Marbled Murrelets in three populations: Southern Oregon, Northern Humboldt county, and the "Bioregion". In this analysis, I used the population modeling program RAMAS GIS.

2. I developed the model based on parameter ranges determined at two workshops in November 1996 and March 1997. Following the procedures established at the workshops, large ranges instead of point estimates were used for all parameters. The parameters of the model are discussed in section 2 (pages 5-17).

3. The assumptions of the analysis are listed in section 3 (pages 17-19).

4. The model simulated the dynamics of the metapopulation by projecting the number of individuals in each of three stages (juveniles, subadults, adults) of each of the three populations for 50 years. The projection was repeated for 10,000 times (replications) to obtain a distribution of possible abundances at each year. These data were then sorted to represent the results in terms of the probability that the metapopulation abundance will fall to a critical level, or a range of abundances. A simplified version of the sequence of calculations made by the program is given in the Appendix (pages 39-42).

5. Sensitivity analysis (pages 19-21) established the relative importance of different assumptions to the outcome (as measured by risk of an 80%) decline within 50 years). Assumptions on vital rates (survival and fecundity) had by far the greatest effect; density dependence, and environmental variation in vital rates also had important effects. Results were moderately sensitive to carrying capacities, catastrophes and correlations. The results were not very sensitive to initial abundances, dispersal, initial distribution to stages, and Allee effects (local extinction thresholds).

6. Effects of logging were modeled under three scenarios: removal of 13%, 27%, or 50% of existing habitat. The impact of logging was very variable depending on the assumptions, and ranged from only 1% increase to 67% increase in the risk of decline to various levels (pages 21-35). The risks were calculated for different levels of decline, because the high variability in the results (originating from the high uncertainties in parameter values) made it impossible to find a critical level (amount of decline) that is appropriate for all comparisons (see section 2.13).

7. Generally, the combination of parameters that predicted low viability also predicted small increases in risk due to logging. Under pessimistic scenarios (low vital rates) the risk of a substantial decline is very high, and logging has little effect, because the populations are already in serious decline for other reasons. Under more optimistic scenarios (high vital rates), the risk of decline is low, and logging effects are more easily detected. When the model predicts that the population is declining fast, then the simulated effect of logging (decrease in carrying capacity in 15 years) does not change the risk very much, because the population size remains well below the carrying capacity for most of the simulation.

8. Because of deficiencies in our knowledge of the ecology of the Marbled Murrelet, and the resulting uncertainties in model parameters, the results of this analysis should not be used as the sole or major basis for making decisions about the conservation of this species. There are several ongoing field studies and data analyses that might potentially be very useful in reducing the uncertainty in several model parameters. These include analysis of offshore counts and inland detections, analysis of habitat relationships, and data from ongoing field studies. Once these data are incorporated into the model, they may help narrow down the range of model results.

9. Long-term monitoring is an important component of a population viability analysis. Monitoring programs should be designed to minimize the uncertainties in the model parameters and to test model assumptions.

10. This analysis was limited to conservation zone 4. Analysis at a smaller geographic scale (e.g., Bioregion) will likely give results that are more sensitive to the simulated effects of logging, whereas analysis at a larger geographic scale (e.g., metapopulation in the listed region) will likely give results that may be more relevant in the context of the viability of the species.

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1 Introduction

This document describes an analysis of the metapopulation dynamics of the Marbled Murrelet in conservation zone 4. The aim of this analysis is to provide input to decisions regarding the impact of a proposed agreement between the U.S. Fish and Wildlife Service and Pacific Lumber Company. In this analysis, I used a metapopulation model that incorporated various aspects of the ecology and demography of the Marbled Murrelet. The input to this model is described in section 2 together with the various model assumptions. The assumptions are also listed in section 3, and model results are discussed in sections 4 and 5.

Because of deficiencies in our knowledge of the ecology of the Marbled Murrelet, and the resulting uncertainties in model parameters, the results of this analysis should not be used as the sole or major basis for making decisions about the conservation of this species. I believe the major contribution of this analysis to the PVA effort is in identifying model parameters and assumptions to which the results are most sensitive, i.e., parameters that are most important in determining the viability of this metapopulation of the Marbled Murrelet.

1.1 Population Viability Analysis

The modeling and risk analysis described in this document is part of an effort to analyze the viability of Marbled Murrelet populations under various assumptions about their ecology and environment, and about the change in their habitat brought about by the proposed agreement. Population viability analysis is a process of identifying the threats faced by a species and evaluating the likelihood that the species will persist for a given time into the future. The process of PVA is closely related to determining the minimum viable population (MVP), which is defined as the minimum number of individuals that ensures a population's persistence. The size of a population is only one of the characteristics that determine the chances of persistence; thus PVA can be thought of as a generalization of the MVP concept. For an introduction to population viability analysis, see Shaffer (1981,1987,1990), Gilpin and Soulé (1986), Boyce (1992), Burgman et al. (1993) and Akcakaya et al. (1997).

There is no single recipe to follow when doing a PVA, because each case is different in so many respects. Some of the components that a PVA might have are field studies, data analysis, modeling, assessment of extinction risks, sensitivity analysis, and monitoring (Figure 1). Not all PVAs will have all these components, and some will have others that are not shown in this figure. The analysis in this report mainly concerns the modeling and sensitivity analysis components of a PVA.
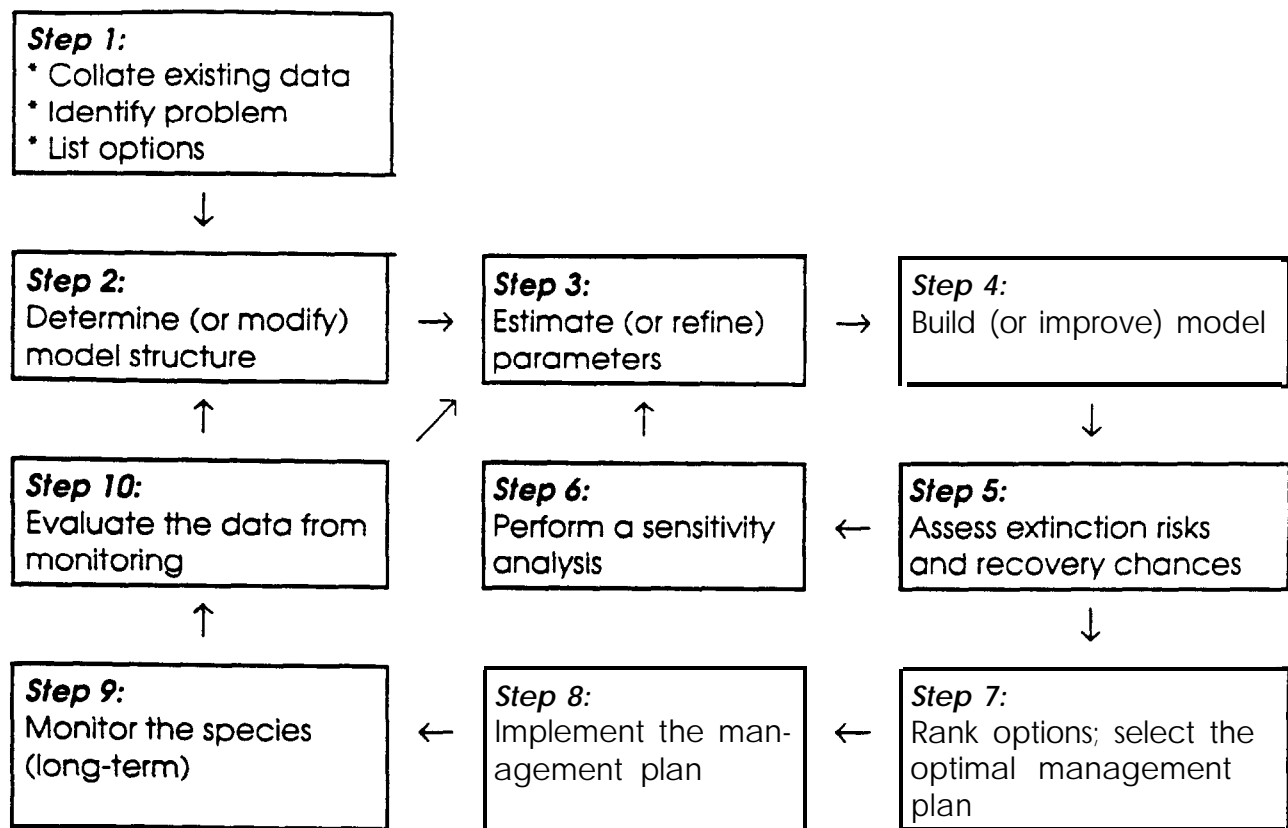
```
┌─────────────────────┐
│ Step 1:             │
│ * Collate existing data │
│ * Identify problem  │
│ * List options      │
└─────────────────────┘
          ↓

┌─────────────────────┐     ┌─────────────────────┐     ┌─────────────────────┐
│ Step 2:             │  →  │ Step 3:             │  →  │ Step 4:             │
│ Determine (or modify)│     │ Estimate (or refine) │     │ Build (or improve) model │
│ model structure     │     │ parameters          │     │                     │
└─────────────────────┘     └─────────────────────┘     └─────────────────────┘
          ↑            ↗            ↑                              ↓

┌─────────────────────┐     ┌─────────────────────┐     ┌─────────────────────┐
│ Step 10:            │     │ Step 6:             │  ←  │ Step 5:             │
│ Evaluate the data from│     │ Perform a sensitivity │     │ Assess extinction risks │
│ monitoring          │     │ analysis            │     │ and recovery chances │
└─────────────────────┘     └─────────────────────┘     └─────────────────────┘
          ↑                                                     ↓

┌─────────────────────┐     ┌─────────────────────┐     ┌─────────────────────┐
│ Step 9:             │  ←  │ Step 8:             │  ←  │ Step 7:             │
│ Monitor the species │     │ Implement the man-  │     │ Rank options; select the │
│ (long-term)         │     │ agement plan        │     │ optimal management  │
│                     │     │                     │     │ plan                │
└─────────────────────┘     └─────────────────────┘     └─────────────────────┘
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Figure 1. Components of a population viability analysis. From Akçakaya et al. (1997), copyright by Applied Biomathematics.

One of the important decisions in building models for PVA concerns the complexity of the model appropriate for a given situation, i.e., how much detail about the ecology of the species to add to the model. Simple models are easier to understand, and more likely to give insights that are applicable in a wide range of situations. They also have more simplistic assumptions, and lack realism when applied to specific cases. Thus they cannot be used to make reliable forecasts in practical situations.

Including more details makes a model more realistic, and easier to apply to specific cases. However in most practical cases, available data are limited and permit only the simplest models. More complex models require more data to make reliable forecasts. Attempts to include more details than can be justified by the quality of the available data may result in decreased predictive power and understanding.

The question of the appropriate level of complexity (i.e., the trade-off between realism and functionality) depends on: (1) characteristics of the species under study (e.g., its ecology), (2) what we know of the species (the availability of data), and (3) what we want to know or predict (the questions addressed).

2 Model parameters

I developed the metapopulation model of the Marbled Murrelets in conservation zone 4 based on parameter ranges determined at two workshops on 22-23 November 1996 (at Lewis and Clark College in Portland, OR) and on 4 March 1997 (at Redwood Sciences Laboratory in Arcata, CA) attended by representatives of various organizations, governmental agencies and companies. In most cases, either the data necessary for estimating the model parameters were not available, or there were large uncertainties. Following the procedures established at the workshops, large ranges instead of point estimates were used for all parameters.

2.1 Modeling platform

In this analysis, I used the population modeling program RAMAS GIS (Akcakaya 1997) developed at Applied Biomathematics. For other applications with this program, see Akcakaya et al. (1995), Akcakaya and Atwood (1997), Akcakaya and Raphael (1998); for reviews of the program, see Kingston (1995) and Boyce (1996). In this analysis, I used only the "Metapopulation model" and "Comparison of results" components of RAMAS GIS When habitat data become available, the "Landscape data" component of the program can be used to provide a link between habitat and demography.

The metapopulation modeling component simulates the dynamics of the metapopulation by projecting the number of individuals in each age class or stage of each population for a specified number of time steps. At each time step, some of the parameters of the model are sampled from random distributions to simulate the effect of environmental fluctuations (see below). The projection is repeated for 10,000 times (replications) to obtain a distribution of possible abundances at each time step. These data are then sorted to represent the results in terms of the probability that the metapopulation abundance will fall to, or exceed, a critical level, or a range of abundances. A simplified version of the sequence of calculations made by the program is given in the Appendix (pages 39-42).

2.2 General model structure

This is a stage-structured, stochastic metapopulation model of the Marbled Murrelets in Conservation Zone 4. The model has three populations: Southern Oregon, Northern Humboldt county, and the "Bioregion". In most of the analysis, these three populations were modeled as three distinct (but interacting) populations of a metapopulation. In one set of simulations, all birds in Zone 4 were also modeled as a single population.

In addition to a Zone 4 model, Marbled Murrelet models discussed in the two workshops included

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(1) a metapopulation model of all Marbled Murrelets in the listed region (CA, OR, and WA; about 7 populations),

(2) a metapopulation model of Marbled Murrelets in CA (about 3-4 populations),

(3) single population or metapopulation model of Marbled Murrelets in the "Bioregion".

The range of 4 models mentioned above (Listed region, California, Zone 4, Bioregion) represent a trade-off in terms of assessing the impact of the proposed agreement: On the one hand, the larger the modeled region, the smaller will be the change in the viability of the species that results from the proposed agreement. This is because the decrease in the number of birds due to the proposed agreement will be a smaller proportion of the total metapopulation size. On the other hand, the smaller the modeled region, the harder it will be to interpret the results in terms of the viability of the species. In this case, the predicted impact will be larger, but it will be harder to evaluate its importance within the context of the species viability. The workshop participants felt that the Zone 4 model was a compromise between these two factors. One or more of the additional models at larger (Listed region and California) and smaller (Bioregion) scales will also be analyzed, but due to time constraints, the first analysis was restricted to the Zone 4 metapopulation.

2.3 **Stage matrix and density dependence**

Each population is modeled in terms of the abundance of Marbled Murrelets in three stages: juveniles (fledglings that have reached the sea), subadults (one-year old birds) and adults (2+ years old birds). This model assumes a simplified life-history of the Marbled Murrelet (Figure 2) in which only adults breed, juveniles become subadults in one year, subadults become adults in one year, and adults remain as adults.
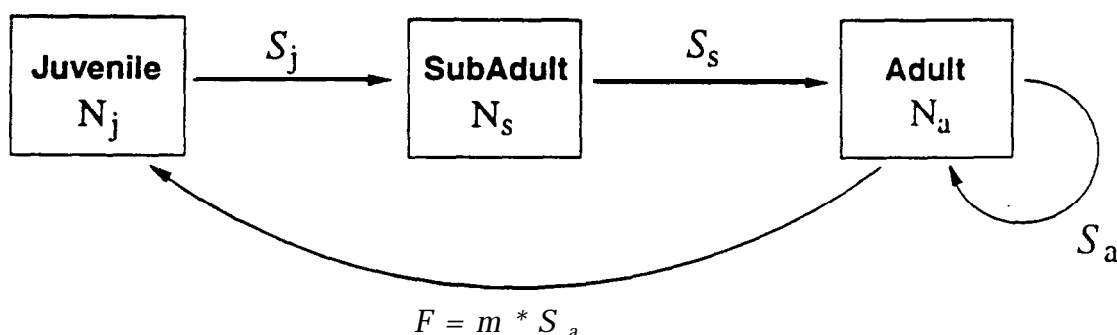

Figure 2. Simplified life history of the Marbled Murrelet.

The model has three dependent variables:

N_j: number of juveniles in the population,

N_s: number of subadults in the population, and

N_a: number of adults in the population.

The parameters of this model are

S_j: the survival rate of juveniles,

S_s: the survival rate of subadults,

S_a: the survival rate of adults, and

F: fecundity.

The model simulates the dynamics of the population in discrete time steps, from **one** year to the next, assuming a "birth-pulse" population, in which all breeding takes place in a short period of time. Changes in the population are updated only once a year. The model assumes a post-breeding census, i.e., updates the abundances of three stages immediately after the breeding season (for an introduction to stage-structured modeling, see Caswell 1989, Burgman et al. 1993, and Akcakaya et al. 1997). In Figure 3, the large black dots represent breeding. The dotted lines represent reproduction, and the solid lines represent the survival of each cohort.
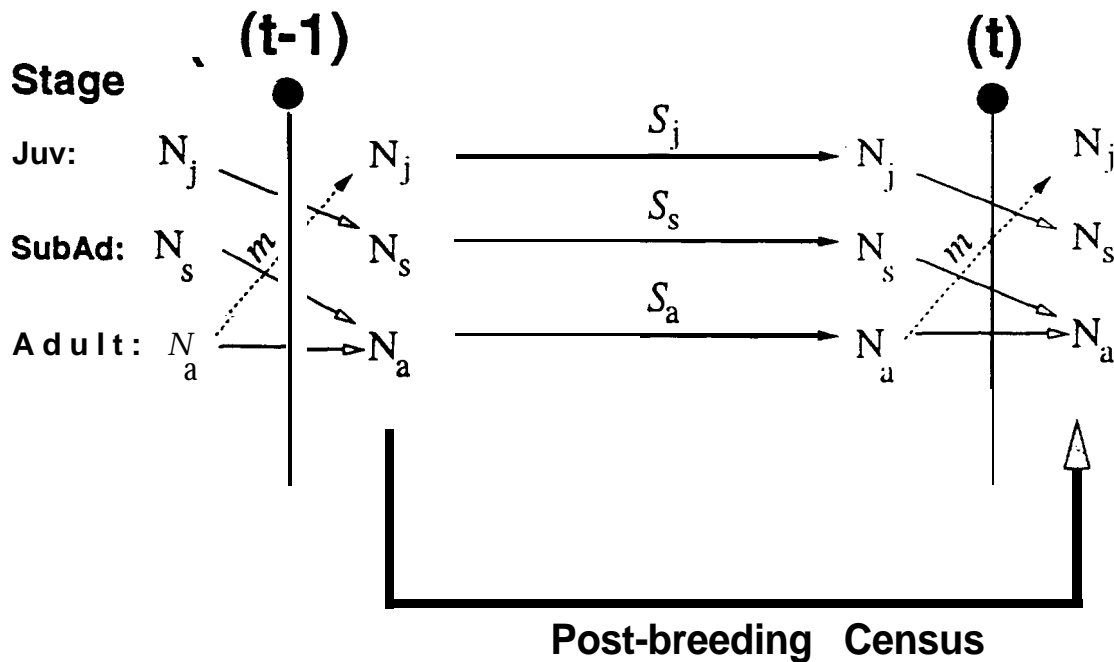
Figure 3. Simplified life history of the Marbled Murrelet with the post-breeding census model.

Fecundity in this stage-structured model is defined as the average number of juveniles reaching the sea, per adult alive at the previous time step. Note that this definition incorporates two types of mortality: the mortality of adults between the last census and the breeding season, and the mortality of juveniles between hatching and the census (which is assumed to occur after juveniles reach the sea). Fecundity is expressed as the product of two numbers: S_a (the survival rate of adults), and m (fertility, or the number of juveniles reaching the sea per adult in the population). Note that:

(1) m incorporates mortality of fledglings before they reach the sea,

(2) m is calculated over all individuals (not pairs or females),

(3) m is calculated over all adults, not just the successful breeders (thus it incorporates the fact that the proportion of successful breeders may be less than 1.0).

The calculations performed by the model for each time step and for each population can be summarized by the following three equations:

$$N_j\ (t+l) = N_a,\ (t) \times F\ (t)$$
$$N_s\ (t+l) = N_j\ (t) \times S_j\ (t)$$
$$N_a\ (t+l) = N_s\ (t) \times S_s\ (t) + N_a\ (t) \times S_a\ (t),$$

where t represents time. The survival rates and fecundity are represented as functions of time to indicate the temporal fluctuations in these parameters (see below). These three equations can be represented by a multiplication of the stage abundances with the following stage matrix. The elements of this matrix (survival rates and the fecundity) are also referred to as vital rates.

	Juvenile	Subadult	Adult
Juvenile:	0	0	$m \times S_a$
Subadult:	S_j	0	0
Adult:	0	S_s	S_a

The range of the parameters of this matrix were based on Beissinger (1995). The range for S_a was [0.875-0.9] and the range for m was [0.12-0.18]. Juvenile and subadult survival rates (S_j and S_s) were assumed to be 70% and 88.8% of the adult survival rate (S_a), respectively.

The stage matrix must be considered in conjunction with density dependence, which describes the changes in the mean values of stage matrix elements as a function of the total abundance in the population. In this analysis, two types of density dependence were used: ceiling-type and contest (Beverton-Holt) type.

In the ceiling type of density dependence, the population grows or fluctuates according to the stage matrix until it reaches the population ceiling, above which the population cannot increase. It then remains at that level until a population decline or fluctuation takes it below this level. If the population grows above the ceiling (by immigration, for example), it declines to the ceiling by the next time step.

In the contest (Beverton-Holt) type of density dependence, the average growth rate of the population depends on the abundance, and not on the stage matrix. If the abundance is low (so that crowding effects of density are minimal), the population grows exponentially. The growth rate gets lower as the population approaches its *equilibrium* abundance, at which level the population growth rate is 1.0 (stable). If the abundance is above this level, the growth rate becomes less than 1.0, and the population declines. Because the population tends to grow when it is low, and tends to decline when it is high, this type of density dependence has a stabilizing effect, which results in lower variability. Thus density-independent models (or models with ceiling-type of density dependence) are often more conservative than contest type of density dependence (Ginzburg et al. 1990).

The contest (Beverton-Holt) type density dependence may arise when the limitation ("ceiling") acts only on the breeding population, and the adults in excess of this ceiling become non-breeders, decreasing the average number of fledglings per adult in the population. In contrast, the ceiling model assumes that all stages are limited; individuals in excess of the ceiling are assumed to be dead. For more information about these two types of density dependence, see Akcakaya (1995; chapter 7), and Akcakaya et al. (1997; chapter 3). For convenience, the population ceiling and the equilibrium abundance mentioned above will both be referred to as the population's carrying capacity although the effect of a change in the numeric value of this parameter obviously depends on the type of density dependence used.

The contest (Beverton-Holt) type density dependence requires an additional parameter (R_{max}, which describes the average rate of population growth when crowding effects of density are minimal. This parameter was estimated by assuming a maximum of 1 fledgling per pair and a 1:1 sex ratio (50% females), i.e., assuming a maximum of 0.5 fledglings per adult. With an adult survival rate of 0.875, this gives a fecundity of 0.875*0.5=0.4375, and with an adult survival rate of 0.9, it gives a fecundity of 0.9*0.5=0.45. These fecundities were then entered into the two stage matrices discussed under (1) and (2) below. The finite rate of increase (eigenvalue) of the two stage matrices with these maximum fecundities were 1.06 and 1.09. These two numbers were used as the R_{max} parameters in the models with contest (Beverton-Holt) type of density dependence. At each time step, the fecundity value was modified by the program so that the average (deterministic) growth rate (eigenvalue of the matrix) was equal to the growth rate determined by the Beverton-Holt density dependence function. Thus, this type of density dependence was assumed to act on fecundities.

In this analysis, five combinations of stage matrix and density dependence were considered:

(1) Ceiling-type of density dependence with the `following stage matrix based on Beis-`
singer (1995):

```
            Juv.        Subad.       Adult
  Juv:     0.0000      0.0000       0.1050
Subad:     0.6125      0.0000       0.0000
Adult:     0.0000      0.7770       0.8750
```

This matrix assumes S_a=0.875 and m=0.12. This model results in an average decline of 7% per year. The decline may be faster, especially at the beginning of the simulated time period, depending on the variation and the carrying capacity (see below).

(2) Ceiling-type of density dependence with the following stage matrix:

```
            Juv.        Subad.       Adult
  Juv:     0.0000      0.0000       0.1620
Subad:     0.6300      0.0000       0.0000
Adult:     0.0000      0.7992       0.9000
```

This matrix assumes S_a=0.9 and m=0.18. This model results in an average decline of 2% per year. The decline may be faster, especially at the beginning of the simulated time period, depending on the variation and the carrying capacity (see below).

(3) Ceiling-type of density dependence with the following stage matrix:

```
            Juv.        Subad.       Adult
  Juv:     0.0000      0.0000       0.1990
Subad:     0.6300      0.0000       0.0000
Adult:     0.0000      0.7992       0.9000
```

The fecundity was set to make the deterministic growth rate (the eigenvalue of the matrix) equal to 1.0. As a result, this model results in a deterministically stationary population (i.e., average growth rate 0% per year). However, because of the ceiling-type of density dependence imposed, the predicted abundance may decline, depending on the variation and the carrying capacity (see below).

(4) Contest (Beverton-Holt) type of density dependence with a stable carrying capacity. In this case, the maximum rate of population growth at low densities (when there are no density effects) must also be specified, and was estimated as 1.06 (6% growth per year) based on an assumption of a maximum of 1 chick fledged per nest, adult survival rate of 0.875, and 1:1 sex ratio.

(5) Contest (Beverton-Holt) type of density dependence with a stable carrying capacity. In this case, the maximum rate of population growth at low densities (when there

are no density effects) must also be specified, and was estimated as 1.09 (9% growth per year) based on an assumption of a maximum of 1 chick fledged per nest, adult survival rate of 0.9, and 1:l sex ratio.

2.4 Initial abundances

The initial abundance, N(O), refers to the total number of birds (of all stages, and both sexes) in each population in the metapopulation. The initial abundances used in the model were based on data from off-shore counts. In the March workshop, the following low and high values were set for the initial abundance of the three populations in the model. The mid values were calculated as arithmetic averages of high and low values.

Population	Low	Mid	High
Southern Oregon	1200	1200	1200
Northern Humboldt	3600	3800	4000
Bioregion	1300	1500	1700

The initial distribution of individuals to stages refers to the proportion of juveniles, subadults, and adults in a population at the start of the simulation. These values do not effect fecundity, survival or any other model parameter. A low proportion of juveniles (6%) was used to reflect the off-shore counts. Most of the simulations were started with 6% juveniles, 12% subadults and 82% adults. In addition, a low-juvenile distribution (0%, l0%, 90%), and a high-juvenile distribution (15%, 9.5% 75.5% based on stable distribution) were used to test the sensitivity of results to the initial distribution of birds to stages.

2.5 Carrying capacities

The population growth of Marbled Murrelets may be limited by food and/or nesting sites. The observed population changes may reflect a deterministic decline to extinction (systemic pressure), **a decline** to a carrying capacity (an equilibrium abundance or a ceiling) that is lower than the current abundance, or fluctuations without a significant trend.

Density dependence was modeled with several models (see above), all of which require a carrying capacity estimate for each population in the metapopulation. In the March workshop, three values were set for the carrying capacity of a population: 75% 100% and 125% of the initial abundance in that population (but see *Cumulative impacts* in section 2.12).

2.6 Allee effects (local extinction threshold)

Another type of density dependence involves Allee effects which may arise from the negative effects of low abundances on the genetics and social structure of the population. Such effects may be modeled by a local (population-specific) extinction threshold, below which the population is assumed to be extinct. Most models used in PVAs ignore Allee effects and do not incorporate local extinction thresholds, effectively assuming a threshold of 0 individuals. Such an assumption is unrealistic, because a small number of birds distributed over a large landscape may not have the same fecundity or survival as a larger population, due to unequal sex ratios, difficulty in finding mates, and behavioral changes resulting from the disruption of the social structure.

In the March workshop two types of local extinction thresholds were set: a low threshold of 1% of the initial abundance and a high threshold of the square root of the initial abundance. The low threshold is proportional to initial abundance while the high threshold represent a larger proportion in smaller populations than in larger populations. In addition to these low and high thresholds, a mid value was used as the arithmetic average of the two values. Once the abundance of a population falls below its extinction threshold, the model assumes all individuals to be dead, and set the abundance of all stages to zero. This is a rather conservative method of incorporating Allee effects.

2.7 Environmental stochasticity (variation)

Environmental stochasticity (variation) refers to the temporal (year-to-year) fluctuations in survival rates or fecundities of Marbled Murrelet populations. Such data are not available for this species. In the March workshop the following low and high coefficients of variation were set. The mid values were calculated as arithmetic averages of high and low values.

Parameter	Low	Mid	High
Survival	3%	7%	10%
Fecundity	20%	35%	50%

Coefficient of variation of a statistical distribution is its standard deviation divided by its mean. These numbers are used in the model to randomly sample survival rates and fecundities in each population at each time step from lognormal distributions that have the means discussed above (see section on stage matrix), and standard deviations derived from these coefficients of variation.

The low and high values listed above represent a wide range for these parameters. One way of narrowing this range down is to use the temporal variation in off-shore counts (or in-land detections) to estimate the variation in fecundity and survival. This may be done by progressively increasing the variation in model parameters until the temporal variation in predicted abundance matches the temporal variation observed in the data. This iterative process necessarily results in a crude and approximate estimate, but might be useful in determining the amount of variation more precisely. The data for this analysis are currently being collated by the Redwood Sciences Laboratory, and will be analyzed for future iterations of this model.

In addition to environmental fluctuations in fecundity and survival, the model will incorporate catastrophes (see below) and demographic stochasticity in survival, reproduction and dispersal. Incorporating demographic stochasticity does not involve additional parameters. It involves selecting the number of survivors (or dispersers) from a binomial distribution with p (probability) equal to the survival (or dispersal) rate, and k (sample size) equal to the number of individuals. A similar procedure is used to sample the total number of fledglings from a Poisson distribution (for more information on modeling demographic stochasticity, see Akcakaya 1991 and Akcakaya et al. 1997).

2.8 Catastrophes

Rare and extreme changes in abundances, survival rates, fecundity or carrying capacities ("catastrophes") may occur due to fires on land, oil spills off-shore, and other marine events. Modeling catastrophes requires three types of information: The probability of the catastrophe (how often it happens), the effect of the catastrophe (how much it decreases abundances, survival rates, fecundity or carrying capacities) and its geographic extent (whether it affects populations singly, or all populations at the same time).

The frequency of such events could be calculated from historical data, e.g.- data on the frequency and impact of oil spills. In this case, such a calculation was not possible, because there were no major oil spills in the modeled region in recent years. In the listed region, there were a total of 15 large and medium oil spills in 25 years, concentrated mostly off northern Washington and central California (Carter and Kuletz 1995). In this model, a range of 0% to 1% per year per population was used for catastrophe probability, and catastrophes were assumed to affect populations singly.

The effect of a catastrophe such as an oil spill is also difficult to quantify. In the *Exxon Valdez* oil spill, direct mortality was estimated to be about 8000 Marbled Murrelets (Carter and Kuletz 1995). Assuming a population of about 89,000 Marbled Murrelets in the Prince William sound, this represents about 9% direct mortality. An oil spill may cause a higher proportional mortality in a smaller population (if the birds are concen-

trated in a smaller area) than in a larger population. In this model, catastrophes were assumed to cause a decline in the abundance of all stages, and a range of 0% to 50% of total abundance per occurrence per population was used for modeling the mortality caused by a catastrophe. Medium values of 0.5% probability and 25% mortality were used as arithmetic averages of the low and high values of the catastrophe parameters.

2.9 Correlation

The degree of similarity (synchrony, correlation) among the year-to-year fluctuations of different populations may have important effects on metapopulation viability. If the variation in vital rates (survival rates and fecundity) are correlated among populations, this may increase the overall variability of the total abundance, and decrease the recolonization chances of extinct populations through dispersal from extant populations (the rescue effect), resulting in a lower viability of the metapopulation than if the vital rates were uncorrelated or independent (Gilpin 1988; Harrison and Quinn 1989; Akcakaya and Ginzburg 1991; Burgman et al. 1993; LaHaye et al. 1994).

Most models used in PVAs implicitly assume a correlation of zero (independent or uncorrelated fluctuations) or one (fully dependent fluctuations). In this case, a correlation of zero may be overly optimistic, considering that large-scale weather patterns probably affect all three populations. In the March workshop, a range of 0.2 to 1.0 was selected to model correlations. The arithmetic average of these two extremes (0.6) was used as a mid-value.

Time series data on in-land detections or off-shore counts from several locations may give clues about the possible range of these parameters. However, such data were not available in time for this analysis. When they become available, they may be analyzed to narrow down the range of correlation coefficients included in the model.

2.10 Dispersal

In this model, dispersal refers to the movement of birds from one population to another at the annual time scale. Dispersal rate is the proportion of birds in the target population that disperse to the source population by the next time step (year).

There are no data to estimate dispersal rates in the zone-4 metapopulation directly. In the March workshop, a range of 0% to 10% total dispersal for juveniles was set (i.e., 0% to 5% of juveniles from one population disperse to each of the other two populations by the next year).   Considering the site-fidelity of alcids, dispersal rate for adults was assumed to be zero, and the dispersal rate of subadults was assumed to be half that of juveniles. The average of the low and high values (e.g., for juveniles, 5% total dispersal, or 2.5% dispersal to each other population) was used as a mid-value.

2.11 Effect of logging

The PVA model is used to analyze the viability of the Marbled Murrelet under two options:

(1) no logging, i.e., current conditions, including cumulative effects (see below), and

(2) logging in part of the Pacific Lumber Company land as specified in the proposed agreement.

In the second case, the effect of logging was modeled as a decrease in the carrying capacity of the model, in proportion to the decrease in total habitat. This effect could be quantified with an analysis of the GIS data on the habitat characteristics. However, such data were not available in time for this analysis. In the absence of such data, the **following range** of habitat (in acres) in each category was suggested by the workshop participants.

	Low	Mid	High
Habitat in currently protected areas:	2000	7000	22000
Habitat in proposed reserve:	500	3177	3177
Habitat to be harvested:	2500	3823	3823
Total habitat in the Bioregion:	5000	14000	29000
Proportion of habitat to be harvested:	50.00%	27.31%	13.18%

Thus the final carrying capacity of the Bioregion population was set to 50% 27% and 13% less **than** the current carrying capacity. These values represent the wide range of opinion on the amount of habitat that would be lost to harvest. As more data are collected, this range of values is likely to decrease. In each of the three cases modeled, the carrying capacity of the Bioregion population was decreased linearly in 15 years from its current value to its final value.

2.12 Cumulative impacts

"Cumulative impacts" refers to the need for incorporating the effects of similar impacts in other parts of a species' range, when assessing the impact of a particular activity. In **this case, in addition** to the loss of habitat in the Bioregion population due to the **agreement mentioned** above, habitat may be lost in the largest population (Northern Humboldt) due to other logging activities. The loss of habitat in the northern Humboldt population was assumed to result in **a** 3% decrease in the carrying capacity of this population. Unlike the logging impact discussed above, this decrease was assumed to take effect immediately.

2.13 Time horizon and metapopulation decline threshold

The results of the PVA are expressed as increases in the risk of decline under logging, from the risk of decline with no logging. Two parameters must be specified for the presentation of these results: the decline threshold (amount of decline) and a time horizon (number of years for which to make the prediction). The time horizon was set at 50 years, because the next 50 years is considered to be the most critical period for Marbled Murrelet populations (U.S. Fish and Wildlife Service 1995). In addition, the uncertainties in the model makes it necessary to limit the time horizon of this analysis. A longer time horizon would give an even wider range of (i.e., even more uncertain) results than in this analysis. A longer time horizon may also decrease the ability of the model to detect human impact, because the model would result in higher overall risk, in addition to more uncertain results, with a longer time horizon. If the risk of decline is high without the simulated logging, the ability of the model to quantify impact due to logging would be diminished.

The decline threshold was not set at a fixed value. The results are expressed in terms of risk of decline as a function of the amount of decline (see Figure 4 for an example), for 4 cases: 0%, 13%, 27%, 50% decline in K (logging impact). Each curve shows, for one these cases, the risk that the total metapopulation abundance will fall by the specified amount (given in the x-axis). For example, the figure shows 4 curves, which give the risk of decline, from bottom to top, with 0%, 13% 27% and 50% decline in K. The bottom curve show that under an assumption of no habitat loss, there is about a 51% risk that the metapopulation will fall to about half of its initial abundance within the next 50 years. Note that this figure is given only for explaining the presentation and interpretation of results. For specific results, please refer to the Results section below.

Because it is rather difficult to view all the graphs at the same time, results were also summarized in tables, in which case, it is necessary to express the risk of decline to a specific level. In tables, the results were presented for two different numerical values of the amount of decline. For sensitivity analysis, this was fixed at 80% decline (i.e., decline to 20% of the total initial metapopulation abundance). For other results, it was specific to each comparison, giving the result for the amount of decline for which the change in risk was maximum. This is necessary because it was impossible to find the amount of decline appropriate for all cases. The right-end of the x-axis in the above figure represents the fixed amount of decline (80% from initial abundance). In this case, the bottom curve indicates that under an assumption of no logging, there is about a 3% risk that the metapopulation will fall to this level within the next 50 years. The vertical bars in the figure show the largest difference between the bottom risk curve (no logging) and other 3 risk curves. For example, the bar between the top and bottom risk curves indicates that if the proposed agreement causes a 50% decline in the carrying capacity of the Bioregion population, then the risk of a 50% decline within the next 50 years will increase from approximately 51% to 77%. The size of the vertical bar is
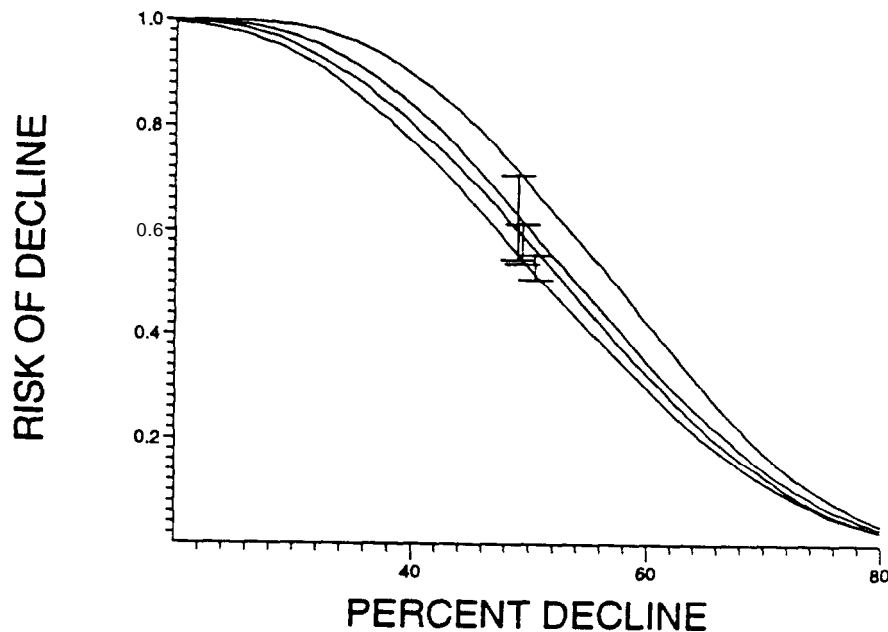
Figure 4. Example of risk curves used in the analysis. The curves show, from bottom to top, the risk of decline under the assumption of 0%, 13%, 27% and 50% decrease in carrying capacity of the Bioregion population (K) due to logging. Each curve shows the risk that the metapopulation abundance will fall by the amount shown on the x-axis, at least once during the next 50 years. For example, in this case there is a very high probability (almost 1.0) of a small (20%) decline, and a low (about 0.03) probability of a large (80%) decline. The vertical bars show the maximal increase in risk due to 13, 27 and 50% decrease in K.

therefore an indication of the maximal effect of logging. Note that these numbers are given only for explaining the presentation and interpretation of results. For specific results, please refer to the Results section below.

Each risk curve is based on 10,000 replications. The 95% confidence interval for the whole risk curve is approximately ±1%, based on Kolmogorov-Smirnov test statistic, D (see Sokal and Rohlf 1981, page 721). The width of the confidence interval is exclusively a function of the number of replications, and does not indicate the reliability or certainty of the model; it only shows the precision of the risk estimates. The uncertainty in the model is represented by the difference between risk curves with the low and high values of each model parameter (see Results below).

3 Assumptions of the analysis

As any model of metapopulation dynamics, this model of the Marbled Murrelet makes a number of assumptions. These assumptions are necessary mostly because of lack of data, but also to keep the model simple enough to be reasonably functional. Most of the assumptions were stated in the description of each parameter in the previous section. Below I list the major assumptions of the model.

1. The metapopulation consists of 3 populations.

2. There is no net dispersal to or from other populations outside this metapopulation, i.e., the rate of immigration and emigration from this metapopulation to other populations of the Marbled Murrelet are equal.

3. Each population consists of juveniles, subadults and adults.

4. The three populations have different initial abundances and different carrying capacities. Otherwise, they all have the same parameters (such as average survival, average fecundity, dispersal, variation in survival and fecundity, density dependence type, maximum rate of increase, etc.), regardless of the quantity and quality of the available habitat.

5. The initial proportion of juveniles in each population ranges from 0% to 15%.

6. Adult survival rate ranges from 0.875 to 0.9.

7. There is no senescence, i.e., adult survival or fecundity does not decrease with age.

8. Subadult survival rate is 89% of adult survival rate.

9. Juvenile survival rate is 70% of adult survival rate.

10. Fecundity ranges from 0.105 to 0.199.

11. Coefficient of variation of survival rate (across years) ranges from 3% to 10%.

12. Coefficient of variation of fecundity (across years) ranges from 20% to 50%.

13. The vital rates (survival rates and fecundity) are fully correlated within each population.

14. Initial number of birds in the Southern Oregon, Northern Humboldt, and the Bioregion populations are 1200, 3600 to 4000, and 1300 to 1700, respectively.

15. The density dependence in these populations can be described either by a ceiling model or a contest (Beverton-Holt) model.

16. In the case of the contest (Beverton-Holt) model of density dependence, the maximum rate of population growth ranges from 1.06 to 1.09.

17. The carrying capacity of the three populations ranges from 75% to 125% of their initial total abundances.

18. Allee effects can be modeled by local extinction thresholds that range from *0.01N* to $\sqrt{N}$, where N is the initial total abundance in the population. Once a population falls to its local extinction threshold, all birds in the population die (the population may become recolonized by dispersers from other populations).

19. Catastrophes occur singly (affect the three populations independently).

20. Probability of catastrophes range from 0% to 1% per year per population.

21. When they occur, catastrophes kill 0% to 50% of all birds in the population.

22. The correlation of environmental fluctuations among populations ranges from 0.2 to 1.0.

23. The total rate of juvenile dispersal from each population (to other populations in the model) ranges from 0% to 10%.

24. The total rate of subadult dispersal from each population (to other populations in the model) ranges from 0% to 5%.

25. Adults do not disperse to other populations.

26. The impact of logging is to decrease the carrying capacity of the Bioregion population linearly in the next 15 years. Logging does not effect other model parameters.

27. The proportion of carrying capacity that will be lost to logging in the Bioregion population ranges from 13% to 50%.

28. The other impacts on habitat consists of a 3% decrease in the carrying capacity of the Northern Humboldt population.

29. There will be no other habitat loss or habitat growth in the next 50 years.

30. Average survival rates, average fecundity, dispersal rates, catastrophe probability and effect, temporal variation in survival rates, and temporal variation in fecundity, will remain unchanged in the next 50 years.

4 Results

The results of the analysis were very variable; the risk that the zone 4 metapopulation abundance will decline by 80% or more in the next 50 years ranged from almost zero to almost one. Section 4.1 describes the sensitivity of results to various parameters and assumptions of the model, and section 4.2 describes the increase in the risk of decline due to logging under various model parameters and assumptions.

4.1 Sensitivity

Sensitivity of the risk of an 80% decline within 25 and 50 years was greatest to vital rates (survival rates and fecundity), density dependence and environmental variation (Table 1). Results were moderately sensitive to carrying capacities, catastrophes and

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correlations. The results were not very sensitive to initial abundances, dispersal, initial distribution to stages, and Allee effects (local extinction thresholds). The results were also not very different between the metapopulation model (with high correlation and medium dispersal) and a single population model.

Table 1. Difference in the risk of an 80% decline in the next 25 and 50 years with the low and high value of each model parameter.

Parameter	25 years	50 years
All parameters	0.9133	0.9999
Survival and fecundity[2]	0.7614	0.9742
Density dependence[3]	0.0123	0.2282
Environmental variation	0.0329	0.1685
Carrying capacity	0.0066	0.0644
Catastrophes	0.0038	0.0623
Correlation	0.0076	0.0558
Initial abundance	0.0014	0.0141
Dispersal	0.0005	0.0049
Initial stage distribution	0.0002	0.0037
Allee effects	0.0006	0.0001
Number of populations[4]	0.0012	0.0017

[1] High refers to the "best-case" scenario; low refers to "worst-case" scenario (see text for details).

[2] Both high and low values assume ceiling density dependence. "Low" refers to the stage matrix (1) discussed in section 2.3, and "high" refers to the stage matrix (3).

[3] "Low" value is ceiling density dependence (2 in section 2.3), and "high" value is contest (Beverton-Holt) type density dependence (5 in section 2.3).

[4] Single population model compared to the metapopulation model with high correlation and medium dispersal.

Each number in the table gives the difference between risk of decline with the low and the high value of the parameter, assuming all the other parameters are at their mid **values** and that there is no logging (i.e., each assume Ceiling density dependence with R=l, 7% C.V. of survival, 35% C.V. of fecundity, 0.5% risk of catastrophes that kill 25% of the population, initial age distribution with 6% juveniles, carrying capacity equal to initial abundances, except 3% cumulative effects in one population, initial abundances equal to 1200, 3800 and 1500 birds in the three populations, 5% total dispersal of juveniles from each population, 0.6 correlation among each pair of populations). The uncertainty that originates from the vital rates (survival rates and fecundity) alone is high enough to make the range of the risk (of an 80% decline in 50 years) almost 0 to 1.

When all parameters were changed to give best-case and worst-case scenarios, risk of an 80% decline within the next 25 years or 50 years ranged from 0 to 1. Best-case scenario refers to high survival and fecundity, contest type of density dependence with R_{max}=1.09, 3% C.V. of survival, 20% C.V. of fecundity, no catastrophes, initial stable stage distribution with 15% juveniles, carrying capacity equal to initial abundances, except 3% cumulative effects in one population, initial abundances equal to 1200, 4000 and 1700 birds in the three populations, 10% total dispersal of juveniles from each population, 0.2 correlation among each pair of populations. Worst-case scenario refers to ceiling density dependence with R=0.93 (i.e., adult survival=0.875 and fecundity=0.l0S), 10% C.V. of survival, 50% C.V. of fecundity, 1% risk of catastrophes that kill 50% of the population, initial age distribution with 0% juveniles, carrying capacity 25% less than initial abundances (minus 3% cumulative effects in one population), initial abundances equal to 1200, 3600 and 1300 birds in the three populations, no dispersal, and full (1.0) correlation among each pair of populations.

4.2 **Impact of logging**

The impact of logging was very variable depending on the assumptions, and ranged from only 1% increase to 67% increase in the risk of decline to various levels. The risks were calculated for different levels of decline, because the high variability in the results (originating from the high uncertainties in parameter values) made it impossible to find a critical level (amount of decline) that is appropriate for all comparisons (see section 2.13).

Generally, the combination of parameters that predicted low viability also predicted small increases in risk due to logging. For example, the worst-case scenario, low survival and fecundity, and ceiling density dependence resulted in high risks of decline, and consequently, low difference in risk of decline between logging and no logging. In contrast, best-case scenario, high vital rates (survival rates and fecundity), and contest density dependence resulted in lower risks of decline, and higher difference in risks of decline between logging and no logging (Figures 5,6 and 7). In these and the following figures, the results are represented in terms of risk curves with 0%, 13%, 27% and 50% decrease carrying capacities due to logging, with the low and high value of the parameter indicated, and with medium values of all the other parameters (except best-case and worst-case simulations, see section 4.1). For a detailed description of how to interpret the results presented in these figures, see section 2.13).
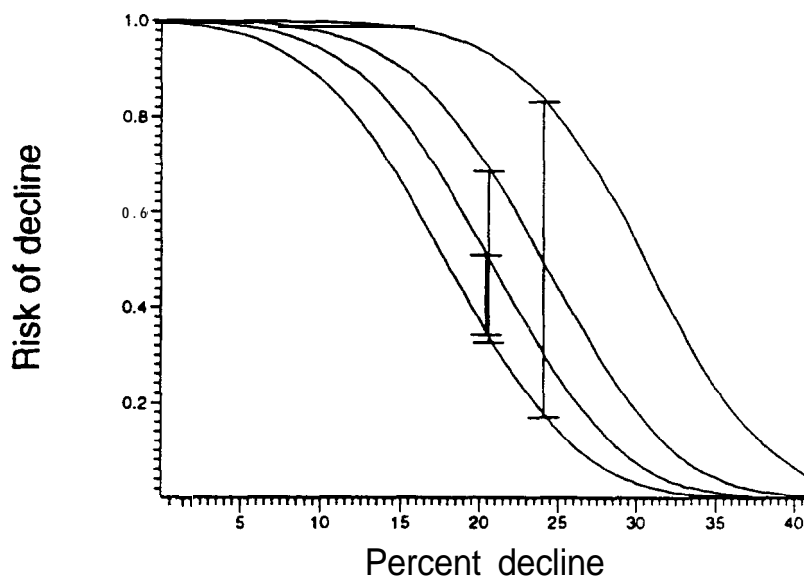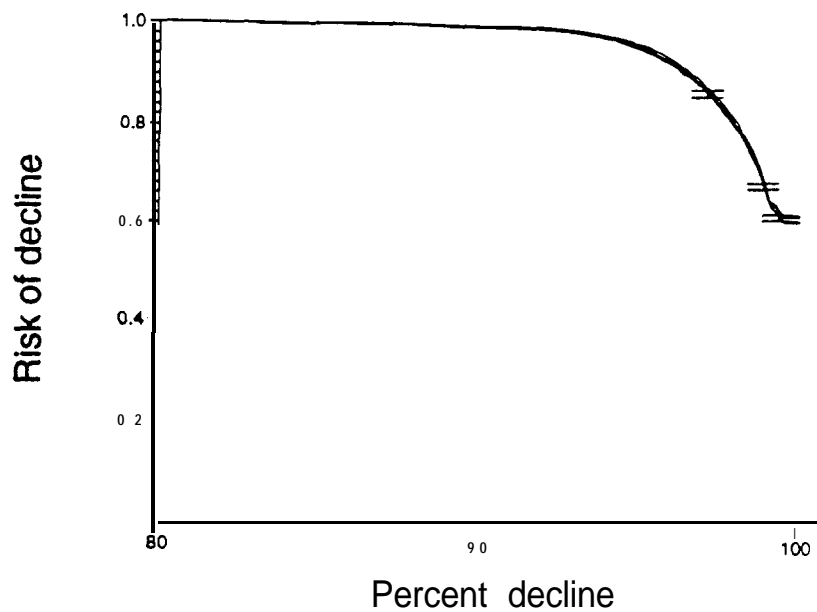
Figure 5. Risk curves with the worst-case (upper graph) and best-case (lower graph) combination of parameters. Note that the x-axis of the two graphs scales are different.

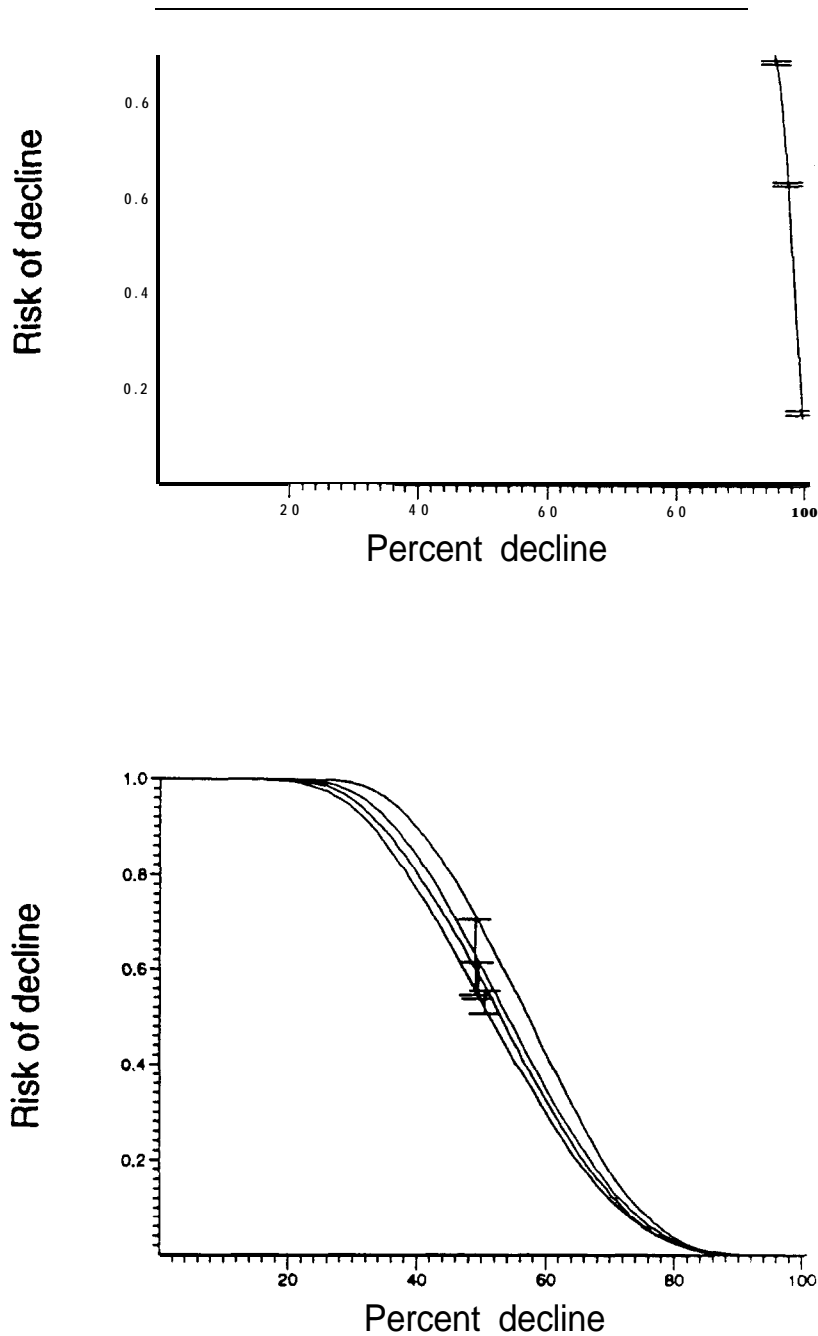# Vital rates (survival rates and fecundity)

Figure 6. Risk curves with low (upper graph) and high (lower graph) values of sur-
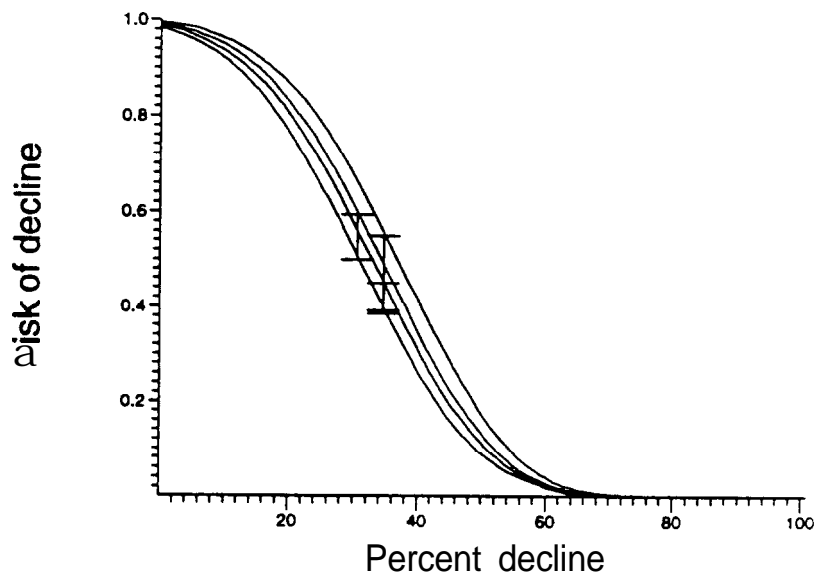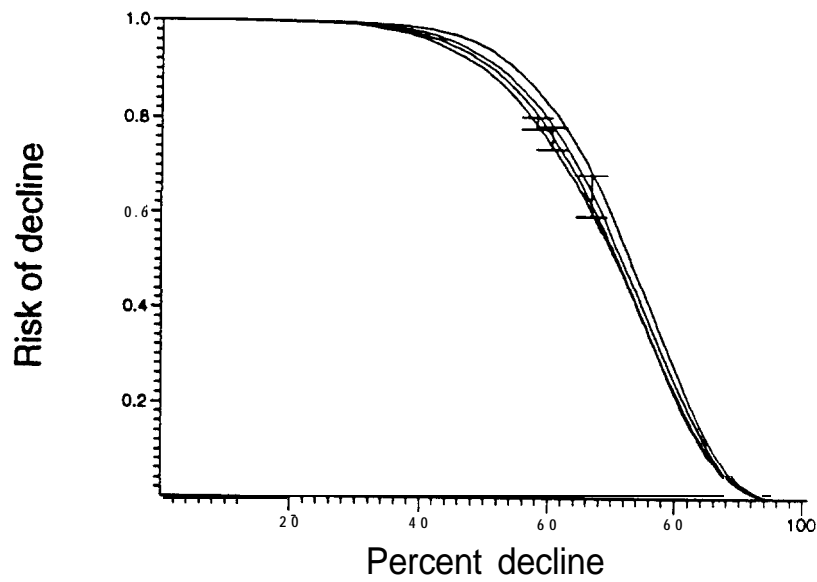vival rates and fecundity.

Density dependence

Figure 7. Risk curves with ceiling (upper graph) and contest (lower graph) type of density dependence.

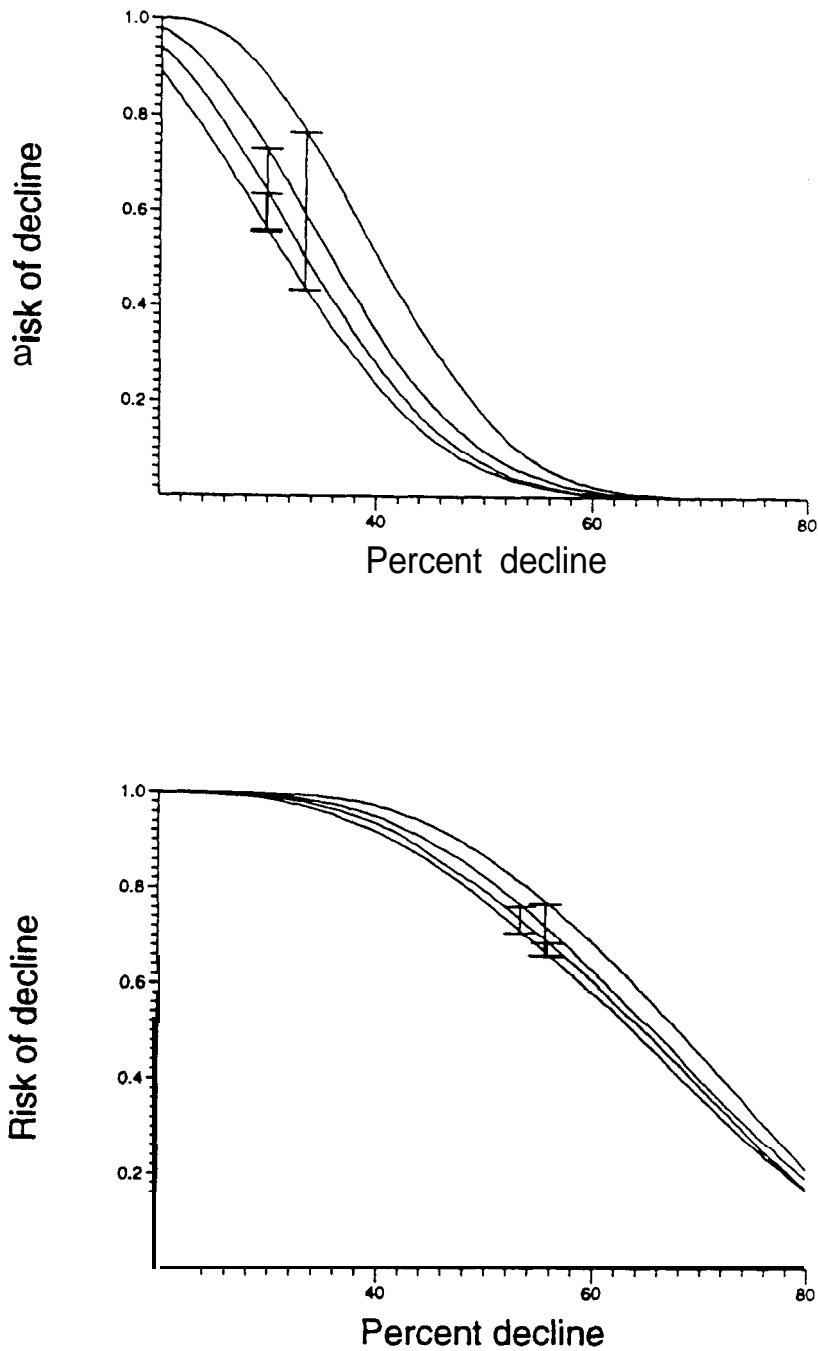*Ecological Risk Analysis for the Marbled Murrelet: The Sensitivity of Viability to the Parameters of the Zone-4 Metapopulation Model. H.R. Akcakaya, Applied Biomathematics, March 1997.*

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Environmental stochasticity (variation)

Figure 8. Risk curves with low (upper graph) and high (lower graph) environmental stochasticity (variation).
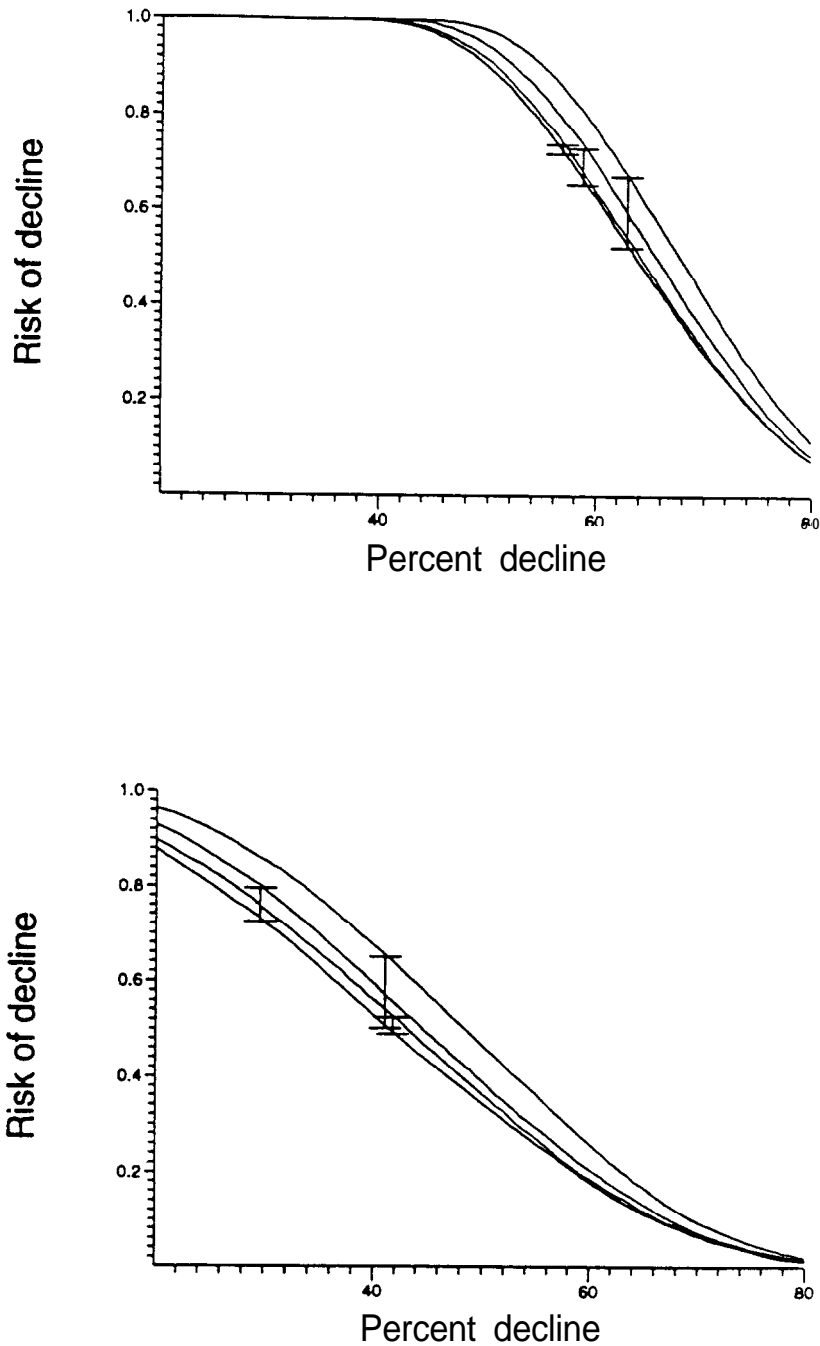
Carrying capacities

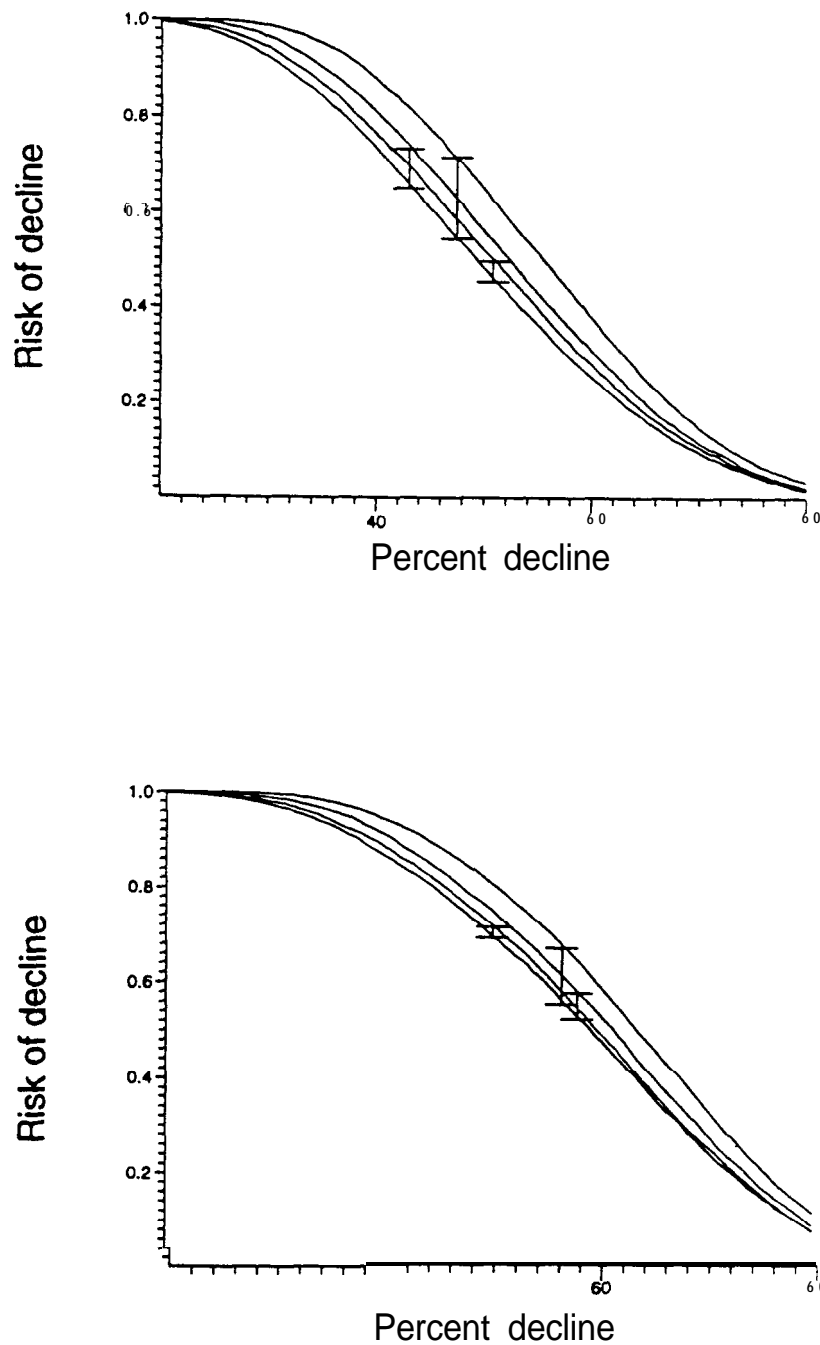Figure 9. Risk curves with low (upper graph) and high (lower graph) carrying capacities.

Catastrophes

Figure 10. Risk curves with no catastrophes (upper graph) and with 1% risk of catastrophes (lower graph).
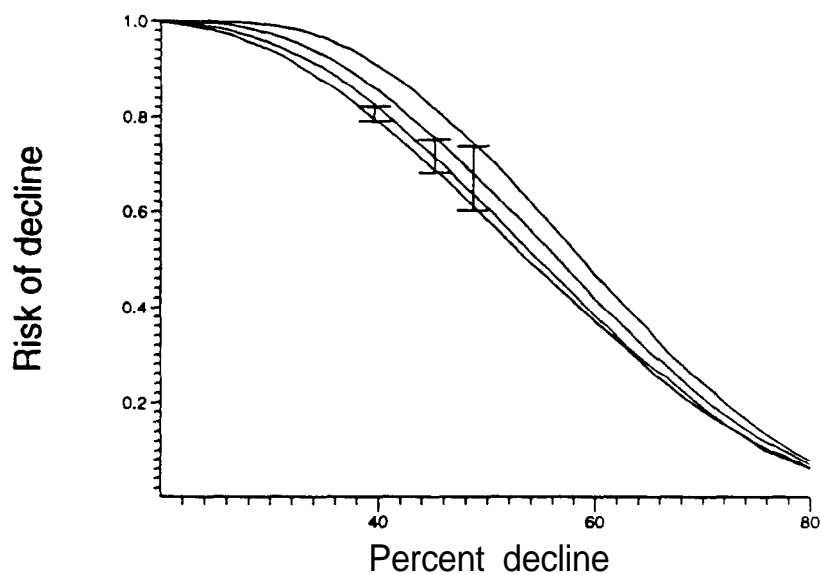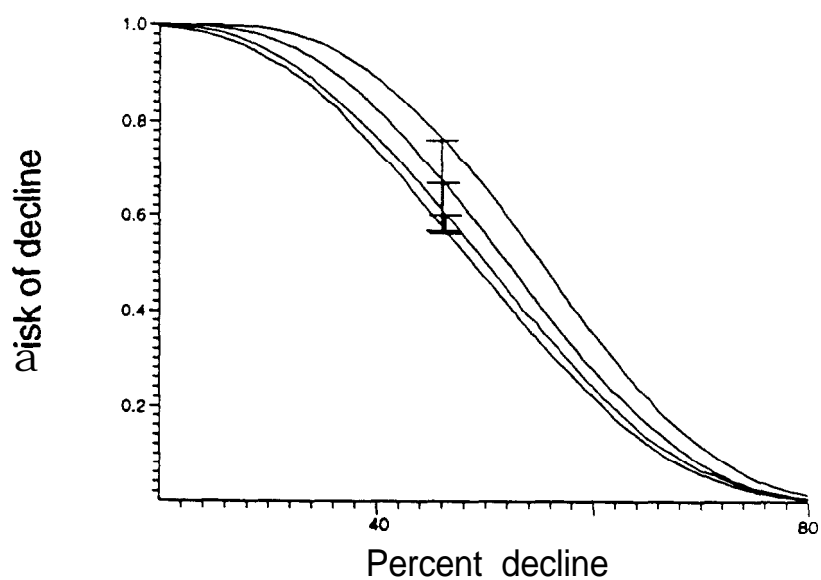
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Correlation

Figure 11. Risk curves with low (upper graph) and high (lower graph) values of correlation.

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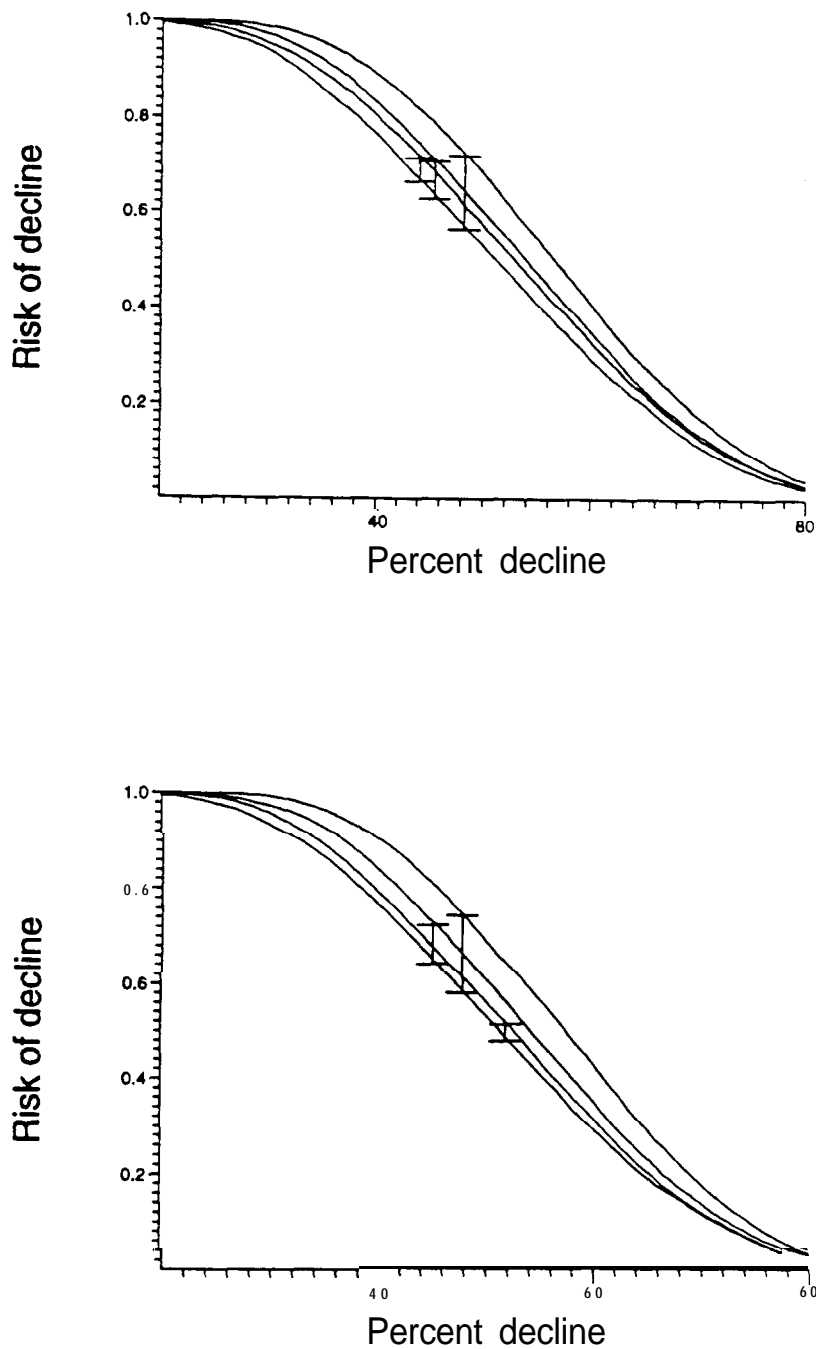
Initial abundances

Figure 12. Risk curves with low (upper graph) and high (lower graph) initial abundances.
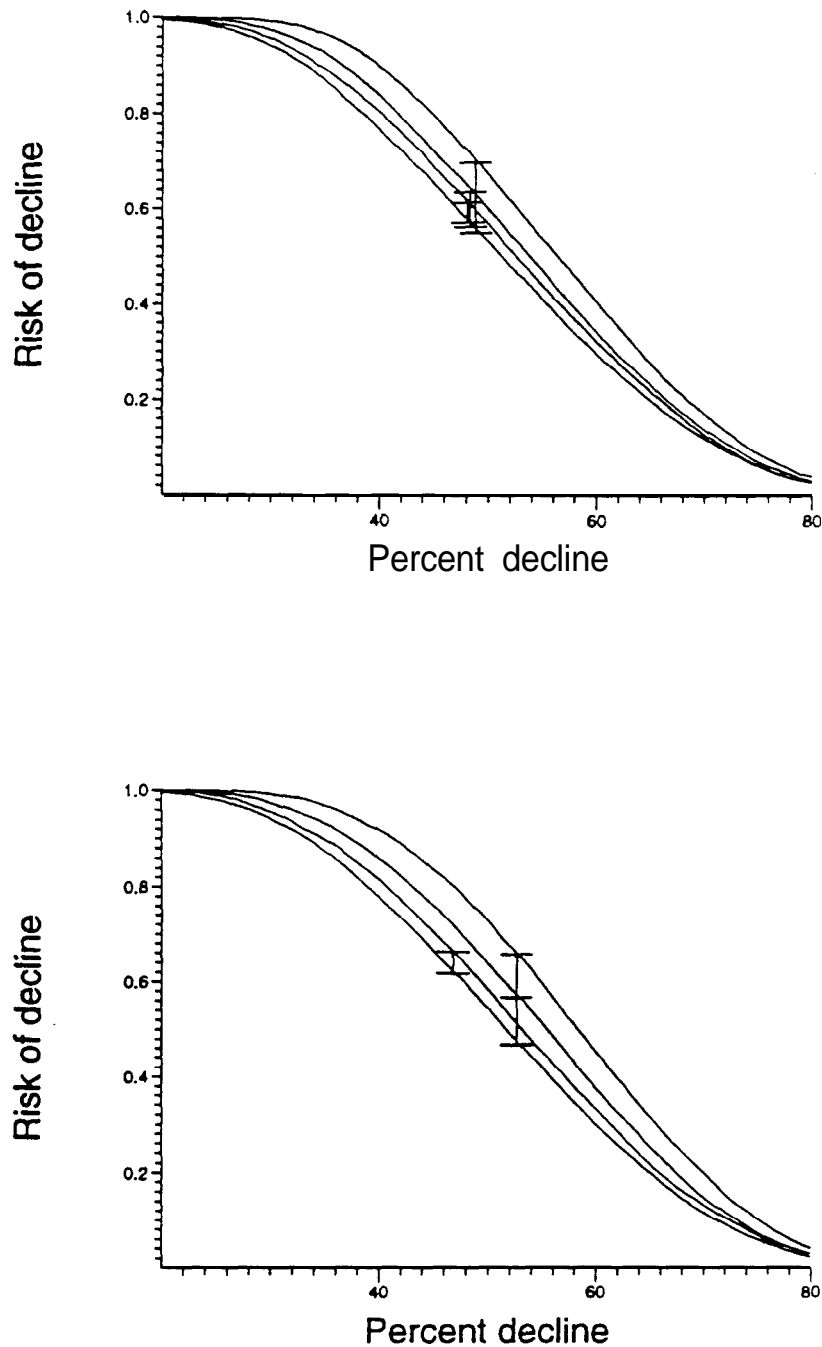
Dispersal

Figure 13. Risk curves with no (upper graph) and high (lower graph) dispersal.
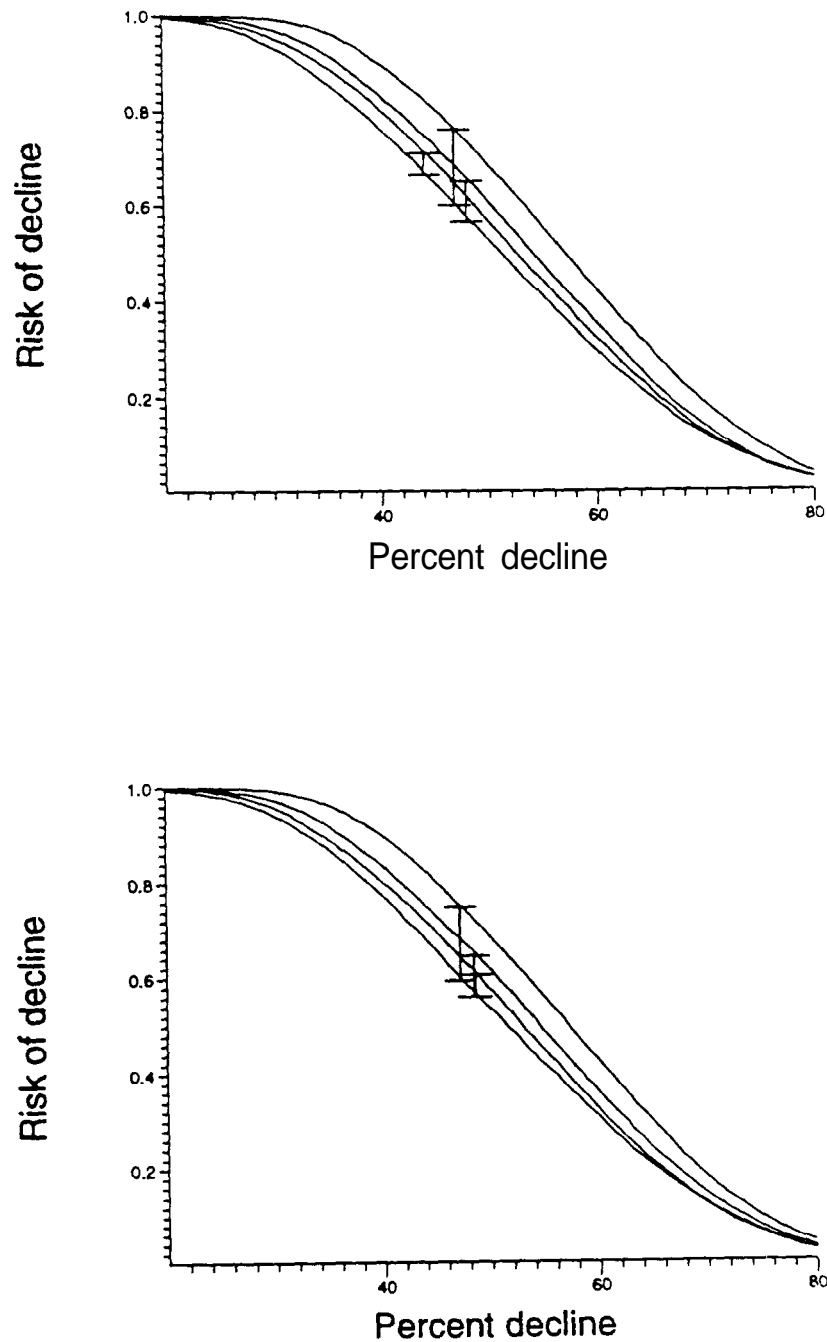
Initial stage distribution

Figure 14. Risk curves with adult-heavy (upper graph) and stable (lower graph) distribution of individuals to stages at the start of the simulation.

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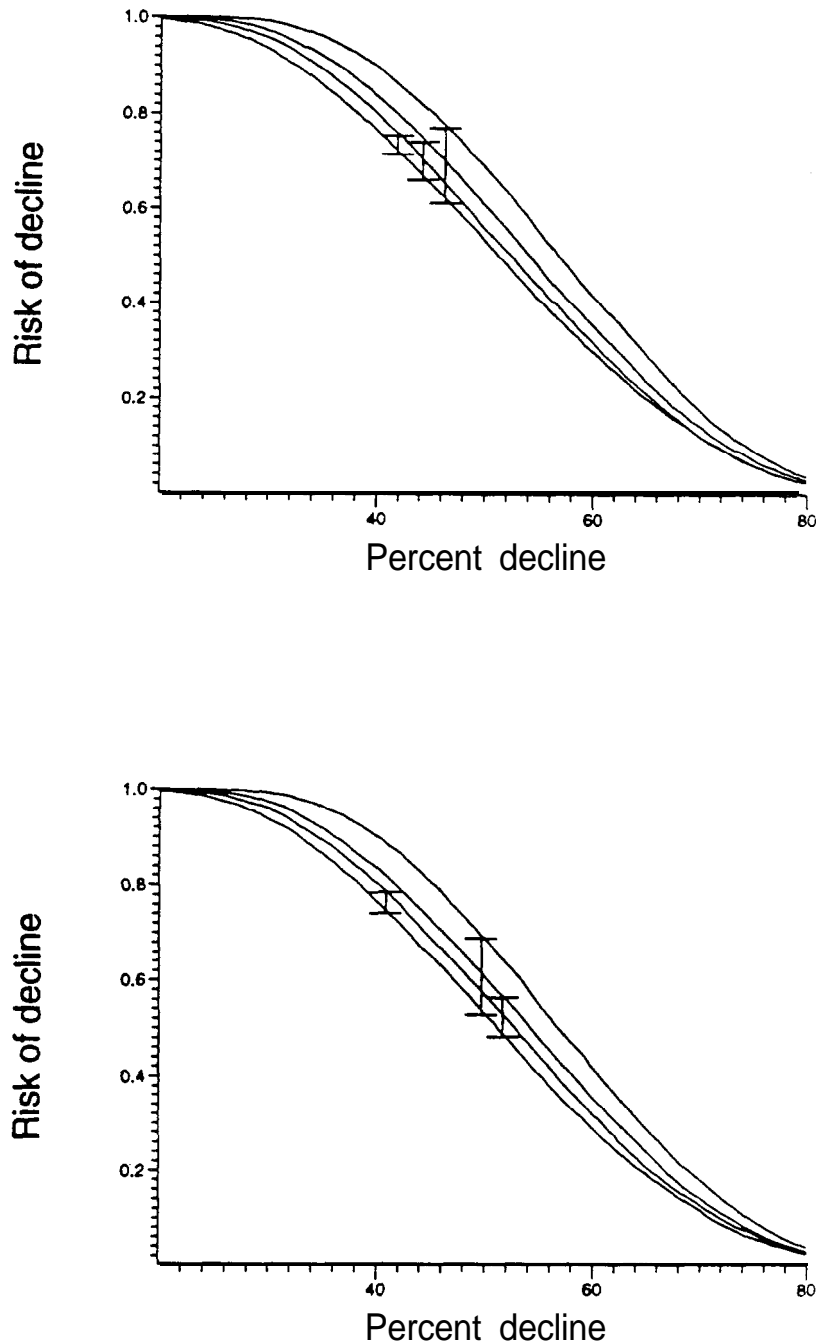# Allee effects (local extinction threshold)

Figure 15. Risk curves with low (upper graph) and high (lower graph) extinction thresholds.
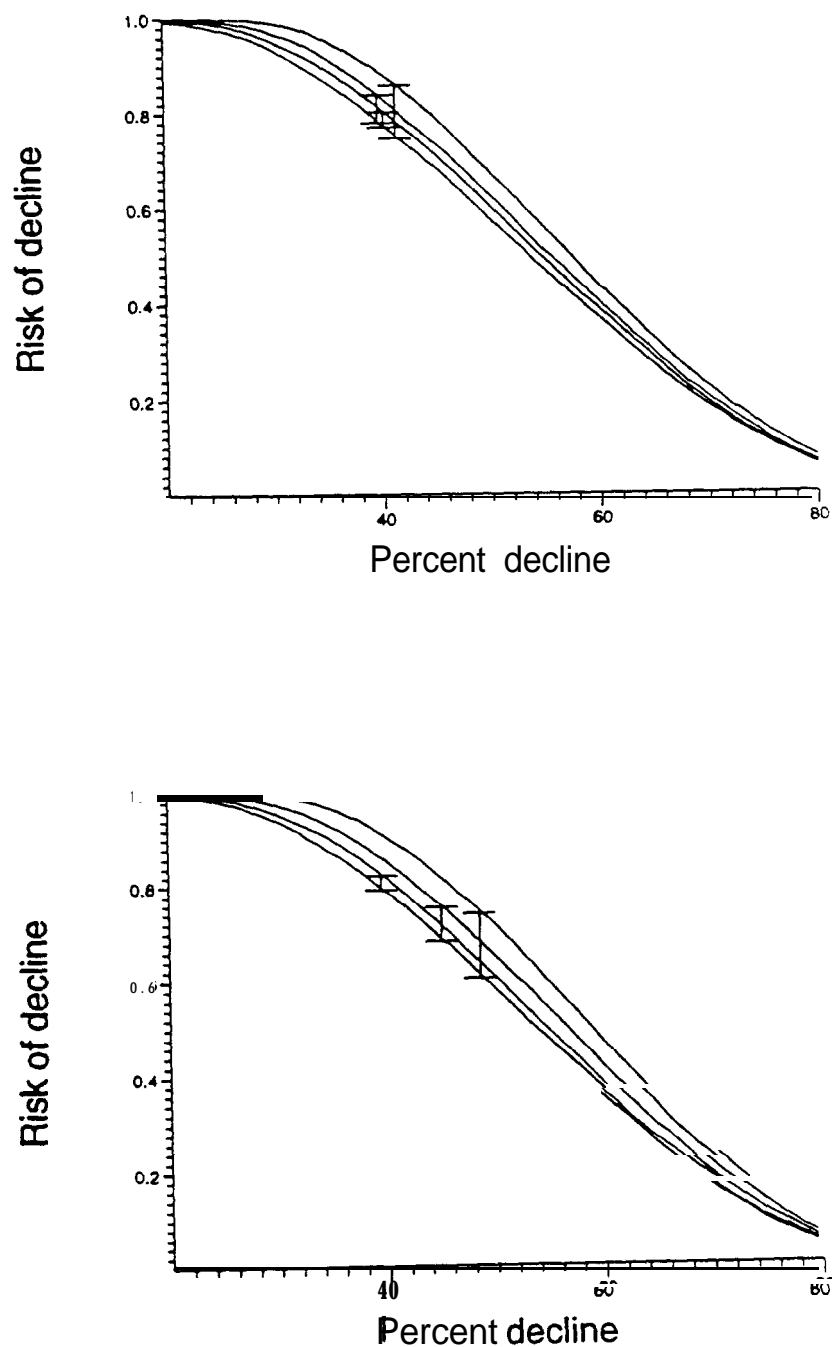
Number of populations

Figure 16. Risk curves with single population model (upper graph) and metapopulation model with high correlation (lower graph).

The results presented in the preceding figures are also summarized in Table 2, which gives, for each model assumption, and for 13%, 27% and 50% decrease in the carrying capacity of the Bioregion population due to logging, the following:

"D":   the increase in risk of decline due to logging (corresponding to the height of the vertical bars in the figures; the risk in this case refers to the risk of a decline of the amount specified in the next column),

"%decl":   the amount of decline as a percentage of the initial abundance (corresponding the x-value or the horizontal position of the vertical bars in the figures),

"Riskl":   the risk without logging (corresponding to the location of the lower end of the vertical bars in the figures; the risk of a decline of the amount specified in the previous column), and

"Risk2":   the risk with logging (corresponding to the location of the upper end of the vertical bars in the figures; the risk of a decline of the amount specified in the "%decl." column).

Note that each risk in this table is the risk of a different amount of decline, so these risks are not comparable to each other. As explained in section 2.13, the amount of decline for each comparison is selected to give the maximum difference between logging and no logging. The reason for this is the difficulty of finding a critical level (amount of decline) that is appropriate for all comparisons, due to the high variability in the results originating from the high uncertainties in parameter values. Thus, the columns D, Risk1 and Risk2 refer to the risk of the amount of decline specified in column "%decl". For example, under the assumption of high local extinction threshold and the medium values of all other parameters (first line in the body of the table), if logging decreased K by 13%, the risk of a 40.8% decline would increase by 0.043, from 0.743 to 0.786, whereas if logging decreased K by 50%, the risk of a 49.7% decline would increase by 0.16, from 0.53 to 0.69.

Table 2. The effect of logging on the risk of decline under various model assumptions and parameters, and three assumptions of the effect of logging on the carrying capacity *(K)* of the Bioregion population. For each assumption, the columns D, Risk1 and Risk2 refer to the risk of the amount of decline specified in column "%decl" (see text for additional explanation and an example).

Assumption	13% decrease in *K*				27% decrease in *K*				50% decrease in *K*			
	D	%dec	Risk1	Risk2	D	%dec	Risk1	Risk2	D	%dec	Risk1	Risk2
Loc.Ext.Thr. high	0.043	40.8	0.743	0.786	0.080	51.7	0.484	0.564	0.160	49.7	0.530	0.690
Loc.Ext.Thr. low	0.040	41.9	0.717	0.757	0.081	44.2	0.663	0.744	0.158	46.3	0.614	0.77 I
Correlation high	0.032	39.7	0.791	0.823	0.072	45.2	0.683	0.755	0.138	48.7	0.603	0.74 I
Correlation low	0.038	46.3	0.563	0.601	0.102	46.0	0.569	0.670	0.194	45.9	0.568	0.762
Vital rates-D.D. 1	0.008	97.2	0.631	0.640	0.010	99.5	0.158	0.149	0.008	95.3	0.886	0.894
Vital rates-D.D.2	0.024	58.3	0.781	0.805	0.047	60.7	0.740	0.787	0.089	67.0	0.598	0.687
Vital rates-D.D.3	0.048	50.5	0.508	0.557	0.077	49.4	0.539	0.617	0.160	49.0	0.547	0.707
Vital rates-D.D.4	0.042	28.9	0.547	0.589	0.086	33.1	0.443	0.529	0.151	32.8	0.454	0.605
Vital rates-D.D.5	0.058	34.7	0.392	0.450	0.095	30.7	0.500	0.595	0.164	34.7	0.385	0.550
Variation high	0.029	55.9	0.657	0.686	0.058	53.4	0.707	0.764	0.110	55.7	0.659	0.770
Variation low	0.081	29.8	0.555	0.636	0.171	29.8	0.561	0.732	0.334	33.4	0.433	0.767
Init.AgeDist no juv	0.046	44.2	0.664	0.710	0.084	48.1	0.566	0.650	0.160	47.0	0.599	0.759
Init.AgeDist stable	0.046	48.7	0.559	0.605	0.086	48.5	0.560	0.646	0.157	47.3	0.592	0.750
Carrying Cap high	0.035	41.8	0.490	0.525	0.072	29.6	0.724	0.796	0.149	41.1	0.503	0.652
Carrying Cap low	0.020	56.8	0.7 17	0.738	0.076	58.7	0.653	0.729	0.150	62.9	0.52 I	0.67 I
Migration none	0.041	48.1	0.573	0.614	0.073	48.3	0.563	0.636	0.147	48.8	0.552	0.699
Migration high	0.045	46.8	0.619	0.664	0.101	52.7	0.467	0.568	0.188	52.7	0.470	0.658
Init. Ahund. high	0.034	52.1	0.483	0.5 17	0.082	45.3	0.645	0.727	0.164	48.0	0.583	0.748
Init. Ahund. low	0.05 I	44. I	0.664	0.7 15	0.079	45.4	0.628	0.708	0.155	48.2	0.565	0.720
Catastrophes none	0.043	50.8	0.454	0.497	0.085	43.0	0.648	0.733	0.170	47.5	0.544	0.714
Catastrophes high	0.024	50.3	0.694	0.718	0.054	58.1	0.525	0.580	0.118	56.7	0.555	0.673
Best-cm	0.168	20.4	0.342	0.510	0.359	20.6	0.327	0.687	0.664	24. I	0.169	0.834
Worst-case	0.012	98.8	0.68 1	0.669	0.012	99.3	0.605	0.617	0.014	97. I	0.858	0.871
Single pop	0.033	40.3	0.772	0.805	0.059	39.7	0.781	0.840	0.113	41.4	0.748	0.860

5 Discussion

The results of the analysis were very variable, as a consequence of the uncertainties in the parameters of the model. The results suggested that the most important parameters determining the uncertainty in predicting the viability of this Marbled Murrelet meta-population are survival rates, fecundity, as well as density dependence and environmental variation in survival rates and fecundity. In addition, carrying capacities, catastrophes and correlations were important determinants of viability. The results were not very sensitive to initial abundances, dispersal, initial distribution to stages, and Allee effects (local extinction thresholds). The results were also not very different between the metapopulation model (with high correlation and medium dispersal) and a single population model, under the assumption of mid-value for the rest of the parameters in both models.

Because of the high uncertainty in parameter estimates, the assessment of the impact of logging gave a very wide range of results. Generally, the combination of parameters that predicted low viability also predicted small increases in risk due to logging. This is expected because the risk of decline can only range from 0 to 1, and if the risk is already high, additional impact due to logging cannot add much to it. If the model predicts that the population is declining fast, then the simulated effect of logging (decrease in carrying capacity in 15 years) does not change the risk very much, because the population size remains well below the carrying capacity for most of the simulation.

Because of deficiencies in our knowledge of the ecology of the Marbled Murrelet, and the resulting uncertainties in model parameters, the results of. this analysis should not be used as the sole or major basis for making decisions about the conservation of this species. There are several ongoing field studies and data analyses that might potentially be very useful in reducing the uncertainty in several model parameters. Analysis of habitat relationships may help reduce the uncertainty in the estimate of the proportion of habitat in areas to be logged. Analysis of off-shore counts and in-land detections may potentially be very useful for several model parameters. It may, for example, give clues about the temporal trend in abundances, which may be used to estimate a narrower range for estimates of fecundity and survival rates. In addition, the temporal variation in these data (year-to-year changes in offshore and inland numbers) may be used to estimate the variability of vital rates (survival rates and fecundity) and their correlation among populations. Ongoing field studies may help estimate adult:juvenile ratios (on which the vital rate estimates are based) more reliably, and may help estimate narrower ranges for other life-history parameters. Once these data are incorporated into the model, they may help narrow down the range of model results.

As indicated in Figure 1 (Step 9), long-term monitoring is an important component of PVA. The results of monitoring give valuable information about the validity of model assumptions, as well as provide more data to refine model parameters and improve the model (Step 10). It is therefore very important that any monitoring program is designed to minimize the uncertainties in the model parameters and to test model assumptions. When a monitoring program is designed purely on a logistical or a statistical basis, its value for improving the viability predictions may be compromised.

The results presented in this report are a function of the many assumptions of the model (see section 3). The sensitivity analysis reported here concerned some of these assumptions, but others were not analyzed due to lack of data, time, or both. For example, the model was restricted to the zone 4 metapopulation. Analysis at a smaller geographic scale (e.g., Bioregion) will likely give results that are more sensitive to the simulated effects of logging, whereas analysis at a larger geographic scale (e.g., metapopulation in the listed region) will likely give results that may be more relevant in the context of the viability of the species. Thus, analyses of the Marbled Murrelet viability at different geographic scales may provide more information about the magnitude and importance of the predicted change in viability due to the proposed agreement.

6 References

Akcakaya, H.R 1991. A method for simulating demographic stochasticity. Ecological *Modelling 54:133-136.*

Akcakaya, H.R 1992. Population viability analysis and risk assessment. Pages 148-157 in D.R. McCullough and R.H. Barrett, editors. *Wildlife* 2001: *Populations.* Elsevier Publishers, London.

Akcakaya, H.R 1994. RAMAS/GIS: Linking Landscape Data with Population Viability Analysis (ver 1.1). Applied Biomathematics, Setauket, New York.

Akcakaya, H.R 1997. RAMAS GIS: Linking Landscape Data with Population Viability Analysis (ver 2.0t). Applied Biomathematics, Setauket, New York.

Akcakaya, H.R and J.L. Atwood. 1997. A habitat-based metapopulation model of the California Gnatcatcher. *Conservation Biology* 11:422-434.

Akcakaya, H.R and B. Baur. 1996. Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. Oecologin 105:475-483.

Akcakaya, H.R and M. Burgman. 1995. PVA in theory and practice (letter). Conserva- *tion Biology 9:705-707.*

Akcakaya, H.R and L.R. Ginzburg. 1991. Ecological risk analysis for single and multiple populations. Pages 73-87 in A. Seitz and V. Loeschcke, editors. *Species Conservation: A Population-Biological Approach.* Birkhaeuser Verlag, Basel.

Akcakaya, H.R and M.G. Raphael. 1998.   Assessing Human Impact Despite Uncertainty: Viability of the Northern Spotted Owl Metapopulation in the Northwestern **U.S.** *Biodiversity and Conservation [in press].*

Akcakaya, H.R., M.A. Burgman and L.R. Ginzburg. 1997. *Applied Population Ecology: principles and computer exercises using RAMAS* EcoLab 1.0. Applied Biomathematics, New York.

Akcakaya, H.R, M.A. McCarthy, and J. Pearce. 1995. Linking landscape data with population viability analysis: management options for the helmeted honeyeater. *Biological Conservation* 73:169-176.

Beissinger, S.B. 1995. Population trends of the Marbled Murrelet projected from demographic analysis. Pages 385-393 in Ralph, C. J., G.L. Hunt, M.G. Raphael, and J.F. Piatt (eds.), *Ecology and Conservation of the Marbled Murrelet.* U.S. Forest Service Pacific Southwest Research Station, Albany, CA.

Boyce, M. 1996. Review of RAMAS/GIS. *Quarterly Review of Biology* 71:167-168.

Burgman, M.A., S. Ferson, and H.R. Akcakaya. 1993. *Risk Assessment in Conservation Biology.* Chapman and Hall, London.

Carter, H.R. and K.J. Kuletz. 1995. Mortality of marbled murrelets due to oil pollution in North America. Pages 261-269 in Ralph, C.J., G.L. Hunt, M.G. Raphael, and J.F. Piatt (eds.), Ecology *and Conservation of the Marbled Murrelets* U.S. Forest Service Pacific Southwest Research Station, Albany, CA.

Caswell, H. 1989. *Matrix Population Models: Construction, Analysis, and Interpretation* Sinauer Associates, Sunderland, Massachusetts.

Ferson, S. and L.R. Ginzburg. 1996. Different methods are needed to propagate ignorance and variability. *Reliability Engineering and Systems Safety 51* (in press).

Gilpin, M.E. 1988. A comment on Quinn and Hastings: extinction in subdivided habitats. *Conservation Biology 2:290-292.*

Ginzburg, L.R, S. Ferson, H.R. Akcakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63-70.

Ginzburg, L.R. and L. Goldwasser. 1997. Variability and measurement error in extinction risk analysis: the northern spotted owl on the Olympic peninsula. In: Ferson, S. (ed.) Quantitative Methods for Conservation Biology. Springer-Verlag, New York (in press).

Harrison, S., and J.F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos 56:293-298.

Kingston, T. 1995. Valuable modeling tool: RAMAS/GIS: Linking Landscape Data with Population Viability Analysis. *Conservation Biology 9:966-968.*

LaHaye, W.S., RJ. Gutierrez, and H.R. Akcakaya. 1994. Spotted owl metapopulation dynamics in southern California. *Journal of Animal Ecology 63:775-785.*

Sokal, R.R and F.J. Rohlf. 1981. *Biometry.* Second edition. W.H. Freeman and Company, New York.

U.S. Fish and Wildlife Service. 1995. Draft Recovery Plan for the Threatened Marbled Murrelet *(Brachyramphus marmoratus)* in Washington, Oregon and California. Portland, Oregon.

Appendix:

Algorithm for **Zone-4 Marbled Murrelet Metapopulation Model**

This appendix gives the sequence of calculations carried out by the metapopulation model during a simulation. This appendix is simplified from Appendix I in Akcakaya (1997) by removing the details that do not pertain to the specific Marbled Murrelet models considered in this analysis. First, a summary algorithm provides a general overview of the model. This is followed by a set of symbol definitions, which are used in a more detailed algorithm. Not shown in these algorithms are various short-cuts designed to increase the speed of calculations and/or reduce memory requirements.

Summa y Algorithm

1. Set up simulation: Check consistency of input data and initialize variables

2. Replications: for each replication, repeat the following steps

   2.1 Initialize population structures from initial abundances.

   2.2 Time steps: for each time step, repeat the following steps

   2.2.1 Produce correlated random deviates

   22.2 Population growth: for each population, repeat the following steps

   2.2.2.1 Local catastrophe - abundances: If there is a catastrophe, reduce number of individuals in each stage

   2.2.2.2 Calculate current carrying capacity according to temporal trend in K (due to logging)

   2.2.2.3 Densitydependence: Set mean transition matrix equal to stage matrix, and modify it according to the specified density dependence

   2.2.2.4 Environmental stochasticity: Sample transition matrix elements from random distribution with modified means and specified standard deviations and correlations.

   2.2.2.5 Project stage abundances with sampling from Poisson and binomial distributions.

   2.2.3 Dispersal

   2.2.3.1 Initialize dispersal variables

   2.2.3.2 For each *source* population, calculate the total number of emigrants from each stage, and update the number of immigrants to each stage of each target population.

   2.2.3.3 For each population, update the number in each stage by subtracting the number of emigrants and adding the number of immigrants.

   2.2.4 Calculate summary statistics for this time step

   2.3 Calculate summary statistics for this replication

3. Calculate summary statistics for the simulation; store results

Definitions for the Detailed Algorithm

CE_p Catastrophe multiplier for abundances of population p (e.g., 0.75 for 2% catastrophe mortality, or 0.5 for 50% mortality).

CL_p Local catastrophe probability for population p (0.005 or 0.01)

K_p Carrying capacity of population *p*

$K(t)$ Current carrying capacity of a population at time t

M_{ip} Dispersal rate from population *p* to population *i*

ND_p Vector of p correlated normal deviates

N_p Total (current) number of individuals in population p

N_{pj} (Current) number of individuals in stage j of population *p.*

NM_{pi} Number of dispersers from population *p* to population i

[*rand*]   A uniform random number between 0 and 1.

R_{max} Population-specific maximum growth rate for contest (Beverton-Holt) type of density dependence (1.06 or 1.09).

SM_j Stage-dependent relative dispersal (1.0, 0.5, 0.0 for juveniles, subadults and adults, respectively).

T_{ij} Transition rate from stage *j* to stage *i* (the vital rate in row *i,* column *j* of the stage matrix).

Other variables and functions are defined locally (in the algorithm).

The symbol prime (') denotes an updated variable.

$x = y$ means that the variable x is assigned to the value of y.

$x < y$ means that if x > y, then the variable x is assigned to the value of y (so that x remains less than or equal to y).

Detailed Algorithm

1. Set up simulation

     1.1 Check stage structure and make necessary corrections:

         1.1.1 All elements of stage matrices and standard deviations matrix must be non-negative.

         1.1.2 Each element of the stage matrix, except those in the first row, must be between 0 and 1, and the sum of such elements in each *column* must be between 0 and 1.

         1.1.3 For each population, the total of all stage abundances must be equal to the total (initial) abundance.

     1.2 Check dispersals

         1.2.1 Each dispersal rate must be between 0 and 1, and total dispersal rate from each population must be less than 1.0.

     1.3 Check correlations

         1.3.1 Correlation matrix must be symmetric and positive-definite.

         1.3.2 Use the correlation matrix to calculate the decomposition matrix that will be used in producing correlated random deviates in step 2.2.1 (see Burgman et al. 1993).

     1.4 Initialize variables for storing results

2. Replications: for each replication, repeat the following steps

2.1 Initialize population sizes and structures from initial abundances; initialize replication variables

2.2 Time steps: for each time step, repeat the following steps

2.2.1 Produce n correlated random deviates: ND,, p=l...n, where *n* is the total number of populations (see Burgman et al. 1993).

2.2.2 Population growth: for each population *p,* repeat the following steps

2.2.2.1 Local catastrophe - abundances
If *[rand]* < CJ_p, reduce number of individuals in each stage:
$$N_{pj}' = N_{pj}\, CE_p\, CS_j$$
and reset counter for time since catastrophe.

2.2.2.2 Calculate current carrying capacity of this population, incorporating its temporal trend (if there is logging):
$$K(t) = KT[p, timestep]$$
where timestep is the number of time steps since the beginning of the simulation, and KT[p,t] is the carrying capacity for population *p* for timestep *t* read from a file.

2.2.2.3 Density dependence.

(i)   Set transition matrix *T* equal to stage matrix for population *p.*

(ii)   For contest type density dependence, calculate deterministic growth rate based on population size at this time step:

$$R(t) = \frac{R_{max}\,.\,K(t)}{R_{max}\cdot N_p - N_p + K(t)}$$

(iii)   For contest type density dependence, calculate constant *m,* which, when multiplied with the transition matrix as described below (in iv), will give a matrix with a dominant eigenvalue equal to *R(t)* calculated above (i.e., will give a growth rate that incorporates effects of density dependence). For ceiling or **exponential** types of density dependence, m = l.

(iv)   Modify mean transition matrix *T* by multiplying with constant *m*:
if density dependence affects all vital rates: $T_{ij}' = m \cdot T_{ij}$, for all columns j, and all rows *i*
if density dependence affects **fecundities:** $T_{1j}' = m \cdot T_{1j}$, for all columns j of row 1
if density dependence affects **survivorships:** $T_{ij}' = m \cdot T_{ij}$, for all columns j, and rows *i*>1.

(v)   Check the consistency of the mean transition matrix (see step 1.1)

2.2.2.4 Environmental stochasticity

(i)   Generate the current transition matrix based on the mean values as modified in steps 2.2.23 for density dependence. If a stochastic simulation, for all columns *j,* and for rows i:
$$T_{ij}' = lognormal(\, T_{ij},\, SD_{ij},)$$
where lognormal (m,s) is a correlated lognormal deviate with mean *m* and standard deviation s (see Ferson and Akcakaya 1990; Burgman et al. 1993).

(ii)   Check the consistency of the realized transition matrix (see step 1.1)

2.2.2.5 Project stage abundances

(i)   project abundances incorporating demographic stochasticity:

$$N_{pi}' = \Sigma_j \, poi(T_{1j} \cdot N_{pj})$$
$$N_{pi}' = \Sigma_j \, bin(T_{ij}, \, N_{pj}), \text{ for } i>1$$

where poi and bin are functions that return random deviates from Poisson and binomial distributions, respectively (see Price et al. 1986). Before N_m, and N_p, are updated, check consistency of projected abundances: $\sum_{j=2} N'_{pj} \leq N_p$.

(ii)   If density dependence is Ceiling, and $N_p > K(t)$, then reduce stage abundances by multiplying each with $K(t)/N_p$.

2.2.3 Dispersal

2.2.3.1 Initialize dispersal variables

2.2.3.2 For each *source* population *p:*

(i)   calculate the total dispersal rate from this population to all target populations i:
$$totmig = \Sigma_i \, M_{ip}$$

(ii)   Calculate current dispersal rate to each target population *i:*
$$M_{ip}' = totmigD/totmig \cdot M_{ip}.$$

(iii)   Calculate the number of migrants, NM_{ji}, from each stage j of this population to each other population *i,* incorporating demographic stochasticity:
NM, =binomial$((M_{ip}' \cdot SM_i), N_{pj})$

(iv)   Check consistency of the number of migrants *NM,,*

(v)   Record total number of emigrants from each stage of this population, and update the number of immigrants to each stage of each target population.

2.2.3.3 Migrate all: For each population p, update the number in each stage j by subtracting the number of emigrants *(E$_{pj}$)* and adding the number of immigrants (I,,):
$$N_{pj}' = N_{pj} - E_{pj} + I_{pj}$$

2.2.4 If a population abundance is below its local threshold, then set all stage abundances in that population to zero. Calculate summary statistics for this time step.

2.3 Calculate summary statistics for this replication

3. Calculate summary statistics for the simulation; store results